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BUTLER UNIVERSITY BOTANICAL STUDIES

VOLUME IV

A QUARTER CENTURY OF BOTANY AT BUTLER UNIVERSITY*

Kingdoms, inventions, masterpieces in literature, art, music, and architecture are born out of dreams. They may seem flimsy and elusive but they show the things which are closest to the heart far down the lapse of time. For, building along the lines of dreams makes realities.

The Butler Botany Department was once upon a time just such an elusive, tantalizingly uncertain dream of a young Ph. D., a dream which occupied his mind when the ink had barely dried on the signatures to his diploma which the University of Michigan had presented to him as tangible evidence of years of intensive preparation for the teaching profession in the field of botany. Excellently equipped, severe in discipline of self, charged with high voltage of enthusiasm for his science, Ray C. Friesner came to Old Butler at Irvington to teach zoology, and to promote the cause of botany. It seems as if of this young Butler professor Chapman wrote:

> "Like clocks, one wheel another one must drive,
> Affairs by diligent labour only thrive."

The foundation dream became a reality, the Botany Department at Butler was established. As the years marched on, Dr. Friesner had other dreams, dreams of a larger department, with greater efficiency and with wider opportunities for the students. These, too, are no longer plans and dreams. New courses, expanding classes, new instructors. Then, new plans, other new courses, new equipment, multiplying files, expanding visions, a growing herbarium, mounting interest in the state flora, a botanical garden, and finally the Butler University Botanical Studies. This publication proved to be a magic tie to bind alumni to the alma mater, a spark to fire the latent power of individual research by the majors in the department, a refiners fire which welded "The Butler Group."

In September 1944 we pause to pay tribute to a quarter century of Botany at Butler, and to look back a moment at the dreams which became realities. And as we review them, garbed in the prosaic form of a report, passing, so to speak, as a chronological batallion, may they

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* A report made to the guests at the anniversary banquet on September 6, 1944.

remind us of the plans, the unflinching faith, and the incessant labor which gave them life.

Dr. Ray C. Friesner was born in Bremen, Ohio, the son of a railroad section foreman. The limited income of the father necessitated that the son himself provide largely the necessary means to acquire a higher education. This he did by sweeping the halls of Ohio Wesleyan. He was an excellent janitor, and he was an honor student.

After graduation from the Bremen high school he chose Ohio Wesleyan for the initial chapter in higher education. Here he came under the influence of the stimulating teaching of Dr. Claude O'Neal, who fired him with that love for botany which has persisted to the present day. For graduate study he selected the University of Michigan, where he worked under direction of Dr. F. C. Newcombe. In 1919 Michigan conferred upon him the doctor's degree. In the fall of the same year Dr. Friesner came to the Irvington campus of Butler University as assistant professor of botany, in the Department of Biology. A new Department of Botany was organized in the first semester of 1920.

The course in general botany, with an enrollment of 43 students, launched his science at Butler. Expansion, however, was the plan from the very start, and so eleven students could avail themselves already in the second semester of a course in trees. During the period of maximum enrollment in the department of 1940-41, The Botany Department had 304 students, with a total of 2,648 student credit hours.

New instructors were added as enrollment mounted. Dr. Stanley A. Cain became instructor in September 1924, Dr. C. M. Palmer joined the faculty in September 1925. In 1928 Mr. Willard N. Clute came to Butler, and the Botanical Garden was laid out. When Dr. Cain, in 1931, joined the faculty of Indiana University, the undersigned became his successor in September 1932. Dr. George Fischer and Mrs. Mabel Esten became members of the teaching staff for temporary service while Dr. Cain was on leave of absence. In 1932 Mrs. Mabel Esten became instructor in the Evening Division. Mr. Scott McCoy was an instructor in the summer session of 1939, 1940, and 1941. He also officiated as assistant curator of the herbarium from 1937 to 1942. In 1941 Dr. Charlotte Grant of Arsenal Technical High School joined the staff of the Evening Division instructors. Temporary positions on the staff were also held by Miss Charlene

Coffing, Mrs. Ina Stanley Fitzgerald, and Dr. Marjorie McConaha Andrews.

Courses offered in 1919 totalled 15 credit hours (three courses), today the Botany Department offers 107 credit hours (25 courses). Butler had no herbarium in 1919, now it possesses an impressive row of metal cases housing over 70,000 specimens of vascular plants. The Department sent out 39,220 specimens to American, European, and Asiatic universities and received 23,220 in exchange. In addition to this collection of higher plants there are 1,700 sheets of algae, and 1,000 packets of mosses.

In 1929 Butler University Botanical Studies made its debut, with Dr. Stanley A. Cain as editor. In normal times it reaches libraries of 167 universities, scattered over the globe. Activity in research is reflected in the 164 books and scientific papers contributed to date by graduate students and members of the staff. The years also brought expansion of the Botany Library, which today receives 240 current publications.

During the first quarter century of Butler University Botany Department 130 men and women majored in botany. Of these, 49 now hold an M. A., and 19 the Ph. D. degrees. Eighteen occupy teaching positions in colleges and universities, and 18 hold membership in the research honor society Sigma Xi. Even though Dr. Friesner has always heeded the admonition of Julius Sachs to his students, "Gentlemen, remember that first of all you are teachers," research was not neglected. The Butler Botanical Studies may be credited, in part at least, with this effort in the search after truth. Dr. Friesner's research interests have cut across many fields in botany, but in recent years stress was placed on the taxonomy of goldenrods (Solidago) of North America, and the growth phenomena in trees (dendrology). Major publications in the field of taxonomy were the monographs of goldenrods of Indiana and of West Virginia. As "watch dog" of Indiana taxonomic reports, and of keeping Deam's Flora of Indiana up-to-date, he has intensified his interest in plants of Indiana, working wholeheartedly and co-operatively with the "grand old man of Indiana flora," Charles C. Deam. Dr. Friesner's field collection numbers have just rounded the 18,669 mark.

Research interests of other members of the Department are diverse and varied. Dr. C. Mervin Palmer centers his attention on the algae of Indiana, and on Lemanea of North America. The undersigned has limited his taxonomic activities to the grasses of Indiana,

and to the plants involved in larger ecological surveys, and specializes in pollen analysis and plant sociology studies.

The smooth operation of the Butler Botany Department is almost automatically controlled by a regular battery of files and up-to-the-minute records which any assistant can handle with ease. The service offered schools by the National Youth Administration of the Federal Government was a blessing to the department in the preparation of extensive cross file bibliographies, and mounting of herbarium specimens.

Dr. Friesner holds membership in ten scientific organizations, whose publications are annually added to the Botany Library. He holds the honor position of "fellow" in A.A.A.S. and in both the Indiana and Ohio Science Academies. In 1936 he served Indiana Academy of Science as president. Working his way through school did not eliminate him from the ranks of Phi Beta Kappa, Phi Kappa Phi, and Sigma Xi. His name appears in the 1941 edition of Who's Who in America, and in 1943 Who's Who in the Western Hemisphere.

The outstanding characteristics of the department are without doubt the harmonious co-operation of members of the staff and the perpetual rejuvenated interest in good teaching and student progress, to which even the research activities must contribute. In normal times the botany majors are regular companions on collecting and bog-boring trips, as well as on excursions when data on ecological and sociological studies are collected. Into the 70,000 plants stored in the Butler Herbarium are woven the student years of our majors. It is not merely a valuable collection of plants; that herbarium made botanists.

And so we stand today on the prominence of a silver anniversary, and pay tribute to labors of by-gone years, but the past holds interest also in that it speeds the work of the future on its way. The plans which lie on Dr. Friesner's desk just now are concerned with the work of the present and the future of Butler University as a whole, and of the Botany Department as an integral part of the university, assigned to him as a special charge.

J. E. POTZGER
Butler 1927

ECHOES

The anniversary activities culminated in a banquet served in the Butler Cafeteria, with Dr. C. M. Palmer as toastmaster. The high-

light of the evening was an address by Professor H. H. Bartlett, head of the Michigan Department of Botany. He spoke on "The Flora of the Pacific." Approximately 100 guests were in attendance. Visitors from other universities were: Dr. Claude E. O'Neal, Ohio Wesleyan; Dr. Paul Weatherwax, Indiana University; Dr. Theo. Just and Dr. Dorothy Parker ('32), Notre Dame University; Professor and Mrs.

Fred Loew, Huntington College; Dr. T. G. Yuncker and Dr. Esther M. Whitney, DePauw University; Mr. Ralph Kriebel and Dr. Alice Withrow ('29) Purdue University, Professor Esther Adams ('25), Moberly Junior College, Moberly, Mo.; Dr. and Mrs. Noe Higinbotham ('35), Texas Agr. Expt. Station, Beaumont, Texas.

<div align="right">J. E. P.</div>

A REPLY

Whatever measure of success there has been in the Botany Department during these twenty-five years, it is certain that the chief contributing factor has been the whole-hearted cooperation of the staff. It has been a privilege to have our share of capable students and this, with devoted teaching, never fails to bring a reasonable degree of success. I should like, also, to express my sincere appreciation to the committee who so successfully "perpetrated" the celebration, to all who had any part in it, to all former students, and to my fellow botanists from other institutions who so generously gave of their time to participate in this celebration.—RAY C. FRIESNER.

A BIOLOGICAL SPECTRUM OF THE FLORA OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK*

By STANLEY A. CAIN

The University of Tennessee

The present study of life-forms of the Great Smoky Mountains flora is based on the system of Raunkiaer (1934). Realizing the difficulties involved in correlation of meteorological and climatological data with the natural occurrences of plants, Raunkiaer designed his life-form system as a means of defining what he called phytoclimates. The theoretical basis was a familiar one in plant geography (Cain, 1944) and may be expressed as follows: (1) Plants are limited in their capacity to endure different environmental complexes. (2) There is usually a correlation between the morphology (growth-form, life-form) of an organism and its environment, *i. e.,* there is a morphological basis for adaptation in many if not all cases. (3) A plant, in its successful existence, represents what may be called an automatic physiological integration of all the factors of its environment. It follows, if these are general truths, that the life-forms of the plants of an area are a measure of the environmental conditions, especially climate. It remains only to find the key to the plant-climate interrelations.

Raunkiaer decided that the significant relationship was to be looked for in the seasonal climates (and all climates but that of the constantly warm-humid tropical rainforest do have a seasonal rhythm in precipitation, temperature, or both). When growth is slowed or dormancy forced upon a plant by cold or drought the most critical tissues are the meristematic. Therefore, the amount of protection provided embryonic growing tissues and their success in enduring the unfavorable period represent a critical adaptation. It is for this reason that Raunkiaer selected the protection afforded the perennating buds as the principal basis for his life-form system.

Raunkiaer's life-form system met with ready acceptance and has been applied widely, if sporadically, over the world. This is because

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the system is homogeneous, the life-forms are relatively few and easily determined, and the results can be employed statistically in the comparison of floras and climates. When the flora of an area is analyzed and it is found that a certain life-form percentage exceeds the proportion which that life-form is of the normal spectrum[1] the phytoclimate is designated by that superabundant or predominating life-form. Thus Raunkiaer spoke of the phanerophytic climate of the tropics, the hemicryptophytic climate of the humid temperate zone, the chamaephytic climate of arctic and alpine regions, and the therophytic climate of deserts.

After forty years there are still insufficient data for a close delineation of the major world climates, but certain general correlations originally pointed out by Raunkiaer have been confirmed, at least for certain regions.

In following Raunkiaer's system in making a biological spectrum of the Great Smoky Mountains flora, I used the preliminary catalogue of the flowering plants of the Great Smoky Mountains National Park, a checklist in preparation for several years under the supervision of Mr. Arthur Stupka, Park Naturalist. The principal field and herbarium work was carried on by the late Professor H. M. Jennison and more recently by Professor Aaron J Sharp. I have not employed the list completely in its present form, having omitted from consideration all varieties and forms except in cases where a species is represented in the area only by a variety. Also, numerous escapes from agriculture and gardens have been omitted where there is any uncertainty as to their establishment. The plant list and my assignment of life-forms to the individual species are not here published because the incomplete nature of the catalogue prevents its release at this time by the Park Naturalist.

In cases where I am not familiar with a species, its assignment to a certain life-form often has been on a basis of previously published classification, usually by Ennis (1928) or McDonald (1937). Cases of questionable life-form status for the Smoky Mountains area and cases of disagreement between authors have been settled by reference to herbarium material and the literature. I am aware of the probability of incorrect assignment of certain species to life-form classes and

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[1] The normal spectrum, based on 1,000 carefully selected species, is no more than a yardstick, a statistical approximation of the life-form percentage composition of the flowering-plant flora of the world as a whole.

hope that the whole flora eventually may be studied in the field from this point of view. Most of the doubtful cases fall on the boundary between geophyte and hemicryptophyte and between hemicryptophyte and chamaephyte. Another need for further field work is in connection with subclasses, particularly among hemicryptophytes and chamaephytes. Finally, life-form studies of the flora of the Smoky Mountains can not be refined greatly without more knowledge concerning the altitudinal occurrences of the species and more complete information concerning the floristic composition of the major plant communities. Since such a thorough-going study may not be possible for years to come, I have assumed that the present preliminary analysis is worth doing for its immediate value.

The five principal classes of the life-form system of Raunkiaer (based, as we have said, on the protection afforded the perennating buds during the unfavorable season) are arranged according to increasing protection: phanerophytes (trees and shrubs), chamaephytes (low perennials with buds close to the ground surface), hemicryptophytes (buds at the soil surface), cryptophytes (buds beneath the soil or under water), and therophytes (annuals, buds within the seeds). These classes are subject to subdivision. The chamaephytes are so few in number that no breakdown was made. My information concerning the hemicryptophytes is inadequate for the detailed treatment of subclasses. The geophytes (the major group of cryptophytes) were classified according to whether the subterranean organs bearing the perennating buds are rhizomes, bulbs, stem tubers, root tubers, or roots, but the various groups seem to have little significance for present purposes. The phanerophytes, however, were easily treated according to four subclasses based on height. Megaphanerophytes exceed 30 meters; mesophanerophytes are between 8 and 30 meters; microphanerophytes are between 2 and 8 meters; and nanophytes are less tall than 2 meters and taller than chamaephytes (about 25 cm.).

The analysis of the flora is found in table I where the total flora, including well-established adventives, is compared with species known to occupy the highest altitudinal belt, essentially from 4,500 feet to the tops of the mountains at slightly more than 6,500 feet. This belt corresponds in general with the altitudinal range of the spruce-fir subalpine forest It is penetrated, however, by northern hardwoods in the valleys and lower gaps, and is interrupted in many places by heath balds (Cain, 1931). In the southwestern portion of the Park

below the southern limits of spruce-fir, the northern hardwoods go to the tops of the mountains and are interrupted by grassy balds. Raunkiaer's normal spectrum is added to table I for comparison.

The flora of the Great Smoky Mountains is conspicuously represented by hemicryptophytes and cryptophytes and is of a type generally referred to the hemicryptophytic climate. It is perhaps more accurate to say that the type of biological spectrum (life-form percentage distribution) here revealed is characteristic of a series of closely related climates of the humid temperate regions with a definite to pronounced winter and continuously favorable growing season. This can be illustrated by placing the spectrum for the Great Smoky Mountains in a series of spectra for eastern North America, table II.

TABLE I

Life-form statistics for the total flora and for the flora of the highest belt in the Great Smoky Mountains National Park.

| Life-form | No. | Total flora | | High altitude species | | | Raunkiaer's Normal Spectrum |
		spp.	Per cent	No.	spp.	Per cent	
Phanerophytes		223	19.5	64		21.2	46.0
(Mega-")	29		2.5	2	0.6		
(Meso-")	73		6.4	18	6.0		
(Micro-")	70		6.1	22	7.3		
(Nano-")	51		4.5	22	7.3		
Chamaephytes		20	1.7	7		2.3	9.0
Hemicryptophytes		595	52.1	170		56.5	26.0
Cryptophytes		173	15.1	52		17.2	6.0
Therophytes		131	11.5	8		2.6	13.0
Totals		1142	99.9	301		99.8	

TABLE II

Some life-form spectra for eastern North America representing areas of humid mesothermal and microthermal climates characterized as hemicryptophytic.

Flora and author Number of species	Phanerophytes	Chamaephytes	Hemicryptophytes	Cryptophytes	Therophytes
Alabama, Ennis, 1928 2,012 species	17.0	3.1	47.8	17.1	14.4
Mississippi, Ennis, 1928 1,724 species	17.7	3.1	49.4	16.2	12.8

TABLE II—(Continued)

Some life-form spectra for eastern North Amercia representing areas of humid mesothermal and microthermal climates characterized as hemicryptophytic.

Flora and author Number of species	Phanero- phytes	Chamae- phytes	Hemi- crypto- phytes	Crypto- phytes	Thero- phytes
Great Smoky Mountains					
1,142 species	19.5	1.7	52.1	15.1	11.5
Bull Run, Virginia, Allard, 1944					
980 species	18.2	1.4	51.7	11.3	17.0
Connecticut, Ennis, 1928					
1,453 species	15.0	1.9	49.4	21.7	11.7
Cape Breton, Ennis, 1928					
637 species	14.1	1.8	51.3	25.6	6.7
Indiana, McDonald, 1937					
2,109 species	14.3	1.9	49.0	18.0	16.7
Iowa, Ennis, 1928					
1,320 species	14.8	1.0	48.6	20.9	14.2
Normal spectrum					
1,000 species	46.0	9.0	26.0	6.0	13.0

Referring again to table I, it is seen that the hemicryptophytic portion of the total flora of the Smokies is 52 per cent, just double that of the normal spectrum. Cryptophytes, with 15 per cent, are two and one-half times the normal. These excesses over the corresponding percentages of the normal spectrum are primarily at the expense of phanerophytes, which are less than half the normal for the world.

That this spectrum is typical of the spectra for the humid temperate climates is seen from the data in table II. These spectra are all of the same pattern and vary only in small ways. The position of the Smokies in the latitudinal series from Alabama and Mississippi to Cape Breton is somewhat misleading because we are here dealing with a mountainous area in which much of the vegetation and the higher climates are characteristic of higher latitudes. Thus the Smoky Mountains spectrum exceeds in hemicryptophytes even that of Cape Breton, and the spectrum for high altitudes in the Smokies (table I) accentuates certain characteristics of the flora as a whole. All the other classes of life-forms are increased at the expense of therophytes. The high position of phanerophytes in the Smoky spectrum (within the series, of course) is an expression of the southern position of the area together with the variation of conditions resulting from the alti-

tudinal range. Its low position for cryptophytes is due entirely to the absence in the mountains of marshes, ponds, and lakes and the consequently very small number of helophytes and hydrophytes.

It is not within the purposes of this paper to discuss life-form spectra in general, especially how the spectra for the hemicryptophytic climate differ from those of steppe, desert, tropical and other climates, but the similarities of the spectra in table II indicate the close similarity in climate of the areas of the deciduous, summer-green forest regions of eastern United States. They do not differ as to the fundamental type of climate, but only in details of length and coldness of winter, etc.

The type of life-form statistics employed in the preceding section depends on the use of total floras of whole areas. In such an analysis one species counts as much as another irrespective of its role in the structure of the vegetation of the area. The other use of life-forms is their employment in the description of vegetation types including communities of all sociological rank. The description of vegetation partly at least in terms of life-form and especially the life-forms of the dominants is an ancient practice in plant geography, as witnessed by such terms as woodland, bushland, steppe, etc. In complex communities the whole phytocoenosis may be referred to in terms of the life-form of the dominating layer. Lippmaa (1933) has developed a system of vegetation description which depends upon the separate analysis of each synusia of the phytocoenosis, the synusiae being single-layered communities each composed of plants of one or of two closely related life-forms. Raunkiaer, however, introduced the most useful, graphically descriptive employment of life-forms in community analysis. I say this because his method uses simultaneously the complete life-form data for the community and statistical information on the quantitative roles of the species. That is to say, he developed life-form spectra for plant communities in which the percentages for each life-form are based on their total frequency points resulting from quadrat analysis. For the Smokies it is possible for me to apply this method only to the cove hardwood forest complex for which some quantitative data recently have been published (Cain, 1943a).

The cove hardwood forest complex is frequently considered to be a unit, especially by foresters, and is sometimes designated as undifferentiated or mixed mesophytic forest by ecologists. Even in the limited Greenbrier area of the Smokies it is, however, recogniz-

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able with close study as consisting of seven minor forest types in two alliances, as follows: Aesculion, including the buckeye-basswood, sugar maple-silver-bell, yellow birch, and beech segregates; and the Tsugion, including the hemlock-beech, hemlock tuliptree, and hemlock segregates. I have statistical data for 31 stands of this complex forest, each sampled by a plot of about one acre area. Sample plot data for the shrub and field layers were obtained from 10 of these stations under spring conditions, and from nine other stations under summer conditions. At each station the vernal flora was sampled by 10 quadrats of one sq. m. area, whereas the aestival flora was sampled by 10 quadrats of six sq. m. area.[1] The cove hardwoods paper cited above contains the results of the quadrat study and presents the results for all the species by constancy and frequency percentages. These long tables will not be repeated here, but they provide the data for the subsequent life-form spectra.

The constancy percentage of a species for a community type is the relationship between the total number of stations studied and the number of stations in which the species occurred in the sample areas. Frequency is the same sort of concept, but it is based on the individual quadrats, rather than on the data for stations.

The following lists of species present the flora of the cove hardwoods as determined by the above procedure, and arranged by life-form. The nomenclature follows Small's Manual and the arrangement in each group is one approximately according to constancy percentages. The resulting life-form statistics compose Table III.

PHANEROPHYTES. Megaphanerophytes: *Tsuga canadensis, Aesculus octandra, Betula allegheniensis, Saccharodendron barbatum, Fagus grandifolia, Fraxinus americana, Liriodendron tulipifera, Padus virginiana, Castanea dentata, Picea rubens, Rufacer rubrum, Tulipastrum acuminatum, Quercus maxima, Quercus montana.*— Mesophanerophytes: *Halesia monticola, Tilia neglecta, Magnolia Fraseri, Acer pennsylvanicum, Hicoria cordiformis, Amelanchier laevis, Ilex opaca, Betula lenta, Wallia cincerae, Cynoxylon floridum, Cladrastis lutea, Oxydendrum arboreum, Robinia pseudoacacia, Parthenocissus quinquefolia* (liana), *Aristolochia macrophylla* (liana).— Microphanerophytes: *Acer spicatum, Svida alternifolia, Hamamelis virginiana, Ilex monticola, Aralia spinosa, Viburnum lantanoides,*

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[1] A brief note on the sampling problem is appended at the end of this paper.

Euonymus americanus, Sambucus pubens.—Nanophanerophytes : *Euonymus obovatus, Hydrangea arborescens, Pyrularia pubera, Grossularia Cynosbati.*

CHAMAEPHYTES. *Alsine tennesseensis, Mitchella repens, Phlox stolonifera, Sedum ternatum, Cymophyllus Fraseri.*

HEMICRYPTOPHYTES. *Tiarella cordifolia, Aster acuminatus, Viola sororia, Viola blanda, Solidago Curtisii, Eupatorium urticaefolium, Nabalus* sp., *Viola hastata, Oxalis montana, Ranunculus recurvatus, Monarda didyma, Poa cuspidata, Osmorrhiza Claytoni, Viola canadensis, Viola rostrata, Galium triflorum, Carex flexuosa, Carex plantaginea, Rudbeckia laciniata, Hepatica acuta, Carex austro-caroliniana, Viola rotundifolia, Cryptotaenia canadensis, Viola eriocarpa, Campanulastrum americanum, Geum canadense, Peramium ophioides, Viola pallens, Viola cucullata, Mitella diphylla, Geranium maculatum, Zizia Bebbii, Juncoides bulbosum, Carex prasina, Ranunculus fasicularis, Micranthes micranthidifolia, Juncoides saltuense, Ranunculus abortivus, Heuchera americana, Senecio Rugelii, Taenidia integerrima, Blephilia hirsuta, Solidago axillaris, Hystrix Hystrix, Houstonia purpurea, Meibomia nudiflora, Juncus tenuis, Thalictrum dioicum, Panicum* sp?, *Carex stellata, Asclepias exaltata, Lysimachia quadrifolia.*

CRYPTOPHYTES (all geophytes). *Erythronium americanum, Dentaria diphylla, Anemone quinquefolia, Urticastrum divaricatum, Bicuculla canadensis, Panax trifolium, Caulophyllum thalictroides, Claytonia virginica, Trillium erectum* var. *album, Cimicifuga americana, Polygonatum biflorum, Disporum languginosum, Tovara virginiana, Hydrophyllum canadense, Medeola virginiana, Validallium tricoccum, Veratrum viride, Arisaema quinatum, Podophyllum peltatum, Xeniatrum umbellulatum, Arisaema triphyllum, Chrosperma muscaetoxicum, Syndesmon thalictroides, Vagnera racemosa, Lilium superbum, Trillium grandiflorum, Actea alba, Diphylleia cymosa, Collinsonia canadensis, Circaea latifolia, Bicuculla cucullaria, Clintonia borealis, Glycine Apios, Monotropa uniflora, Carex pennsylvanica.*

THEROPHYTES. *Impatiens pallida, Galium circaezans, Cuscuta* sp., *Adicea pumila, Phacelia fimbriata, Galium aparine.*

Lines 1-3 of table III present life-form spectra for the cove hardwoods in which the species as such form the basis of the statistics. The total flora spectrum, line 1, differs strongly from that for the Park as a whole, table I. Phanerophytes increase from 19.5 to 36.3 per cent, a change that would seem to be due to the fact that this is a

very rich forest community (14 mega-, 15 meso-, 8 micro-, and 4 nanophanerophytes) in primeval condition with rather uniform microclimatic and soil conditions under the arborescent dominance. The second conspicuous change from the spectrum for the whole Park is from 15.1 to 25.8 per cent cryptophytes. Chamaephytes likewise are increased, from 1.7 to 4.4 per cent, but these figures are too small to be of much consequence. The increases are at the expense of the hemicryptophytes, which drop from 52.1 to 30.1 per cent, and therophytes, from 11.5 to 3.4 per cent.

TABLE III

Life-form spectra for the primeval cove hardwoods of the Smokies.

		Ph	Ch	H	Cr	Th	
	Spectra based on species						Species
1.	Total flora	36.3	4.4	30.1	25.8	3.4	113
2.	Field layer, vernal aspect	. . . .	7.0	47.2	40.3	5.5	72
3.	Field layer, aestival aspect	. . . .	6.6	61.3	29.3	2.6	75
	Spectra based on constancy						Points
4.	Total flora	31.1	5.9	33.1	26.9	3.0	4,052
5.	Field layer, vernal aspect	. . . .	9.0	48.0	39.0	4.0	2,790
6.	Field layer, aestival aspect	. . . .	8.1	58.1	31.1	2.7	2,877
	Spectra based on frequency						Points
7.	Field layer, vernal aspect	. . . .	11.0	43.3	41.9	3.8	1,309
8.	Field layer, aestival aspect	. . . .	14.2	58.6	23.9	3.3	1,258

When the phanerophytes are left out of consideration and the herbaceous synusia is considered alone there naturally are percentage changes, so comparison will be made only between the vernal and aestival aspects of this layer. The most striking result is the pronounced representation of cryptophytes in the vernal flora (40.3 per cent, and all geophytes) and the preponderance of the more slowly developing but ultimately rank-growing hemicryptophytes in the aestival flora (61.3 per cent). The contrast between six per cent cryptophytes for the normal spectrum, 15 per cent for the whole Smoky Mountains flora, and 40 per cent of geophytes alone for the vernal flora of the cove hardwoods is a very striking phenomenon.

Seven geophytes in the vernal flora which were absent in the aestival aspect, apparently because of having rapidly completed their life-cycle and retreated again to their subterranean organs, are *Erythronium americanum, Bicuculla canadensis, Bicuculla cucullaria, Panax*

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trifolium, Claytonia virginica, Trillium grandiflorum, and *Actea alba.*
The seven other geophytes unsampled in the aestival flora are the
longer enduring *Veratrum viride, Podophyllum peltatum, Lilium
superbum, Diphyllcia cymosa, Collinsonia canadensis, Circaea latifolia,*
and *Clintonia borealis.* The six geophytes sampled in the aestival
flora and not in the vernal flora are *Tovara virginiana, Chrosperma
muscactoxicum, Syndesmon thalictroides, Glycine Apios, Monotropa
uniflora,* and *Carex pennsylvanica.* Although the differences in
geophyte listing for the vernal and aestival aspects of the field layer
are partly due to sampling and partly due to normal variability in
composition of such a rich community, it still seems that the first
group of species listed immediately above represents a distinct excess
of geophytes in the vernal flora. Furthermore, that the cryptophyte-
hemicryptophyte relationship in the vernal and aestival societies is
a true one is substantiated by the constancy and frequency studies
(lines 4-8, table III) where very similar ratios reoccur.

It often happens that the use of quantitative data for species in
the development of life-form spectra produces strikingly different
results from spectra based solely on species with each species having
the same weight. In this case, however, the various field spectra are
all of the same pattern, as shown by lines 2, 5, and 7 for the vernal
aspect and lines 3, 6, and 8 for the aestival aspect. This result would
seem to be due to the fact that the cove hardwoods flora is a very rich
one in which no small number of species is clearly predominant. This
situation is in strong contrast to the more impoverished but compar-
able field layers of the mesophytic deciduous forests of Europe
(Lippmaa, 1938, and Raunkiaer, 1934). The most interesting new
feature of the compared spectra (obtained from species alone, con-
stancy points, and frequency points) is the steady increase of chamae-
phytic percentages from 7.0 to 9.0 to 11.0 for the vernal aspect and
from 6.6 to 8.1 to 14.2 for the aestival aspect.

Theoretically the most significant spectra for the microphytocli-
mate of the field layer of the cove hardwoods are those based on fre-
quency points because they provide better data on the roles of the
species in the community. Raunkiaer showed that frequency points
approach density values when numerous small quadrats are used.
The best way of preparing statistical life-form data for spectra would
probably be by the use of dominance data because of the biological
significance of dominance in a community, but such information is

not at hand for the cove hardwoods. At any rate, the spectra based on frequency points are more revealing as to the role played by the various life-forms than are the spectra based on species composition alone.

In table IV are spectra on certain American forest associations the data for which I believe to be comparable. The two spectra for mixed mesophytic climax are strikingly similar. The communities would appear to be wholly comparable ecologically and probably are climatically, the higher altitude of the Tennessee stands compensating for the higher latitude of the Ohio stands. The Long Island oak "association segregate" has a conspicuous increase in chamaephytes which is maintained by the Laurentian maple "association segregate" and to which is added a striking increase in hemicryptophytes. These trends at the expense of phanerophytes and cryptophytes, and within the deciduous forest climax formation, are in accord with expectation according to Raunkiaer's theory of phytoclimates and experience with regional spectra. The two studies on *Populus* associations also produce similar spectra. Although the data are fragmentary, there is a suggestion that association spectra may be used better to distinguish climatic differences and delimit types than areal and regional spectra. Specifically, spectra based upon floras as large as those of states, or even areas like Cape Breton and the Great Smoky Mountains, include too much variability of microclimate and habitat for any but the most general comparisons.

One technical point concerning the quadrat technique may be added here as a sort of appendix, and that concerns the use of different sizes of quadrats in the sampling of the vernal and aestival aspects of the field layer. I have discussed this problem elsewhere (Cain, 1932, 1938, 1943b), but these data offer a new approach. Notice in table III that the constancy points for the vernal aspect are 2,790 and for the aestival aspect 2,877 although the sampled area in the latter was about six times that of the former. The same relationship holds for the frequency points where the numbers are 1,309 and 1,258, respectively. No such close approximations could have resulted had constant-size quadrats been used in the sampling of both aspects. The larger size for the aestival aspect was necessitated by the larger stature and area of the summer plants.

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TABLE IV

Life-form spectra of certain American deciduous forest associations.

	No. Species	Ph	Ch	H	Cr	Th
Cove hardwoods mixed mesophytic climax, Great Smoky Mountains	113	36.3	4.4	30.1	25.8	3.4
Mixed mesophytic climax, Cincinnati area. Withrow, 1932	127	33.6	3.9	34.4	23.4	3.9
Quercetum montanae, Long Island, New York, Cain, 1936	92	34.8	10.9	32.6	20.6*	1.1
Aceretum saccharophori, Laurentian region. Dansereau, 1943	346	17.0	10.0	56.0	15.0	2.0
Aspen association, Northern Lower Michigan. Gates, 1930	310	22.9	3.9	47.1	16.1	10.3
Poplar association, Central Alberta. Moss, 1932	170	25.8	1.8	48.2	17.1	7.0

* Including 2.1% Monotropaceae.

SUMMARY

1. The life-form spectrum for 1,142 species of the Great Smoky Mountains National Park is entirely similar in pattern to other spectra for humid mesothermal and microthermal climates and the eastern American deciduous summergreen forest region. Hemicryptophytes predominate, being the life-form of 52 per cent of the total flora.

2. Species of the area known to exceed 4,500 feet elevation and grow in what is essentially the spruce-fir belt produce a similar spectrum to that of the Park as a whole, but with all classes slightly increased at the expense of therophytes which drop from 11.5 to 2.6 per cent.

3. Statistical data (on constancy and frequency) for the flora of the virgin cove hardwood forests of the Greenbrier region of the Park allowed a special analysis of life-forms in that community:

a. In comparison with the Park as a whole, the cove hardwoods show an exceptionally high percentage of geophytes (25.8%), and a high percentage of phanerophytes (36.3%) for the latitude.

b. Comparison of the vernal and aestival aspects of the herbaceous layer of the cove hardwoods showed the importance of geophytes in the vernal flora (40.3%) and of hemicryptophytes in the aestival flora (61.3%).

c. Spectra obtained from constancy and frequency points are entirely of the pattern of ones from species *per se*. This is due to the large number of species involved and the lack of preponderance in numbers and mass by one or a few species.

4. A comparison of certain forest-association spectra reveals close similarity between closely related associations, such as the Southern Ohio and Eastern Tennessee mixed mesophytic associations and the Alberta and Michigan *Populus* associations. The Laurentian *Acer* "association segregate" reveals the influence of more northern position in its relatively high Ch and H percentages better than does a regional spectrum in the case of Cape Breton.

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THE STEM SMUTS OF STIPA AND ORYZOPSIS IN NORTH AMERICA[1]*

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Over much of that great natural resource called the "Western Range," comprising some 728 million acres (1), species of *Stipa* and *Oryzopsis* are prominent and important members of the grass cover. These are commonly found affected with stem smut; often as much as 15-20 per cent of the plants are affected, and occasionally as much as 90 per cent infection is encountered. In view of the value of these grasses as components of the western range, and the general interest manifest in the nature of the stem smuts so common on them, it seemed desirable to make a study of the identity of these smuts. It soon became apparent that more smut species are responsible for stem smut on *Stipa* and *Oryzopsis* than had hitherto been recognized as occurring in North America. Also it became evident that for more than 80 years stem smuts of *Stipa* and *Oryzopsis* have been collected and curated in this country under the name *Ustilago hypodytes* (Schlecht.) Fr., while as a matter of fact six distinct species and one variety, in two genera were really represented. The various morphologic aspects of the complex of stem smut fungi masking under the name *U. hypodytes* on a wide variety of grasses all over the world already have been presented (4). The present paper is a taxonomic treatise on the known fungi causing stem smut in *Stipa* and *Oryzopsis* in North America. The following key will serve to differentiate them.

KEY TO THE STEM SMUT FUNGI ON STIPA AND
ORYZOPSIS SPP. IN NORTH AMERICA[3]

1. Spores in definite, persistent, large balls.................*Urocystis fraserii*
1. Spores free 2
   2. Spores small (3.5-7μ), smooth and unadorned....................... 3
   2. Spores larger (6-14μ), exospore rough, cracked, verruculose, or lobed
      or echinulate at opposite poles.................................. 4
      3. Sori covered by persistent membrane of fungus tissue..........
      .... *Ustilago minima*
      3. Sori naked after emerging from leaf sheath....*Ustilago nummularia*[4]
         4. Spores large (10-14μ), verruculose............*Ustilago jacksonii*
         4. Spores smaller (6-10u), more or less bipolar.................. 5
            5. Spores with a cracked exospore often resulting in an ear-like
               appendage at opposite poles..............*Ustilago williamsii*
            5. Spores with a crest of echinulations or merely with apically
               thickened wall at opposite poles.......................... 6
               6. Spores yellowish to olivaceous-brown, finely papillose to
                  minutely echinulate; bipolar areas minutely echinulate
                  to echinate ....*Ustilago spegazzinii*
               6. Spores dark-brown, smooth or very finely papillose;
                  bipolar areas consisting of smooth apical thickenings...
                  ....*U. spegazzinii* var. *agrestis*

1. USTILAGO MINIMA Arth. Bull. Iowa Agr. Coll. Dept. Bot. 1884:
172. 1884.

Sori surrounding the internodes, aborting the inflorescence, covered by a
persistent whitish membrane of fungous tissue; spores escaping from ruptured
or detached ends of membrane, spherical, light brown, smooth, 3.5-5μ. Fig. 1,
A; fig. 3, A; fig. 6, A.

On: *Oryzopsis hymenoides* (Roem. and Schult.) Ricker   Ariz.,
Colo., New Mex.

Stipa comata Trin. and Rupr.   Neb.
Stipa neomexicana (Thurb.) Scribn.   Ariz.
Stipa spartea Trin.   Iowa, S. Dak.
Stipa sp.   Calif., Colo.

This species has been much confused in the various herbaria with
the next species, *U. nummularia* (*U. hypodytes* Auct.).   There ap-
pears to have been a tendency to consider the membrane as evanescent,
and therefore of little taxonomic value.   Hence many herbarium speci-

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[3] Examination under oil immersion lens is recommended in connection with
microscopic characters mentioned in this key.
[4] See also *U. spegazzinii* var. *agrestis*.   Some collections of this variety
have inconspicuous bipolar areas and might be keyed out as *U. nummularia*.
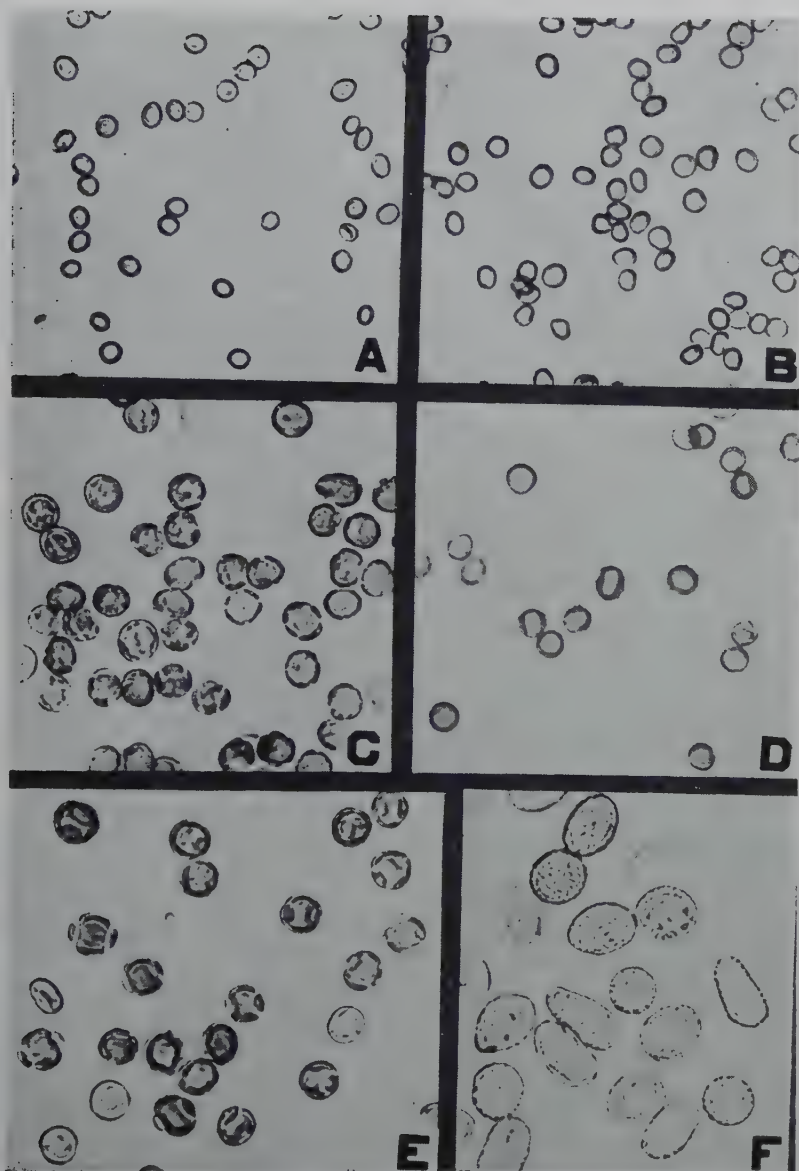
Figure 1. Photomicrographs of the chlamydospores of the species of *Ustilago* causing stem smut on *Stipa* and *Oryzopsis* in North America. A. *Ustilago minima;* B. *U. nummularia;* C. *U. williamsii,* form with cracked exospore but few appendages; D. *U. spegazzinii;* E. *U. williamsii,* form with appendages open; F. *U. jacksonii.* x approx. 600.

mens have been encountered which had been entered as *U. minima* and which clearly belong in *U. nummularia*. The membrane which surrounds the sorus in *U. minima* is not evanescent; on the contrary it is a tough, persistent membrane of fungous tissue in the specimens I have examined. As pointed out by Clinton (3), Arthur did not mention this membrane, although it is present in his specimens.

Germination of the spores has not been observed. Fresh material or recent collections were not available.

2. USTILAGO NUMMULARIA Speg. An. Mus. Nac. de Buenos Aires. (ser. 3) 1: 59. 1902.
Ustilago hypodytes Auct.
Sori surrounding the internodes and sometimes extending into the aborted inflorescence, naked except for enveloping leaf sheaths, dusty, dark brown to almost black; spores globose to sub-globose, yellowish to olivaceous-brown, smooth, chiefly 4-5μ in diameter, or 3-4 x 4-5μ. Fig. 1, B; fig. 3, B; fig. 6, B.

On: *Oryzopsis hymenoides* Colo. Idaho, Mont., Utah, Wash., Wyo., Sask.
Stipa comata Calif., Idaho, Mont., Ore., Wash., Wyo.
Stipa neomexicana N. Mex.

Stipa sp. Calif.

This stem smut is most common on Indian Rice Grass, *Oryzopsis hymenoides,* and needle grass, *Stipa comata.* High percentages of infection have been observed in Washington, Oregon, southern Idaho, and northern Utah, occasionally running as high as 90 per cent.

Ustilago nummularia has only recently been recognized as occurring in North America. Fischer and Hirschhorn (4) showed that this species is one of several often erroneously referred to *U. hypodytes.*

Spore germination in *Ustilago nummularia* has been described by Fischer and Hirschhorn (l.c.), and is illustrated in fig. 2, C & D.

3. USTILAGO SPEGAZZINII Hirsch. Notas del Museo de La Plata, Botanica 4: 415-419. 1939.
Caeoma hypodytes Schlecht. Fl. Berol. 2: 129. 1824. (in part).
Ustilago hypodytes Auct.

Sori chiefly surrounding the internodes, but sometimes also involving more or less the inflorescence, although usually the latter is entirely aborted, olive-brown to dark brown, entirely naked except for the enveloping leaf sheaths; spores globose to sub-globose or slightly ovoid, provided with bipolar sub-hyaline crests consisting of a prolongation of the epispore into a group of echinulations,

finely papillose to minutely echinulate, clear yellowish-brown to olivaceous-brown, mostly 4-6μ in diameter, or 3.5-4 x 4-7μ. Fig. 1, D; fig. 4, A; fig. 6, C.

On: *Stipa mucronata* HBK. (*S. setigera*) Mexico

Stipa spartea Ill., Iowa, Wisc.
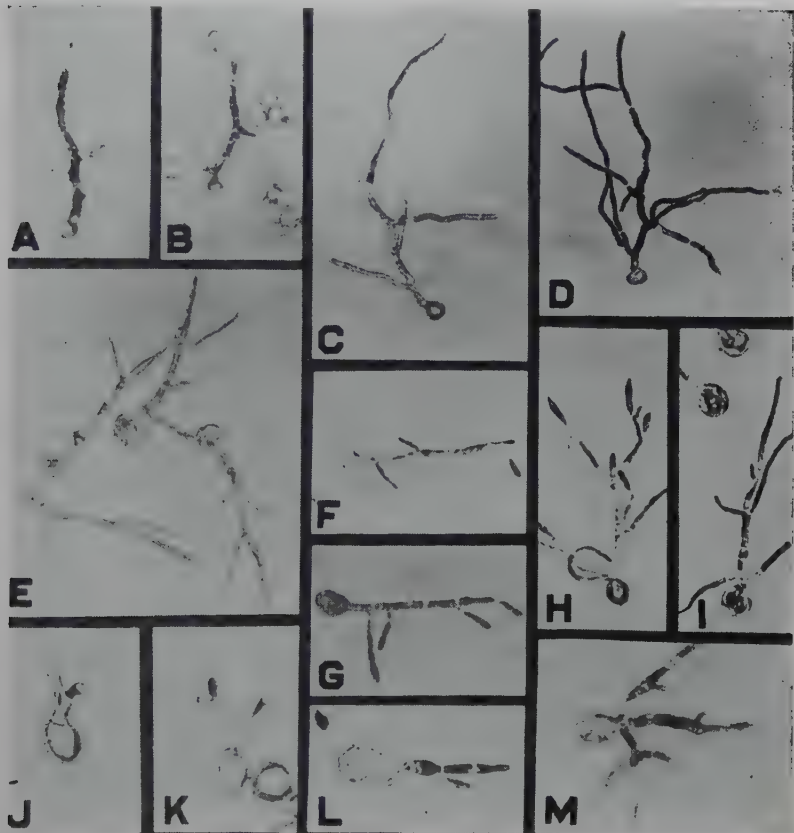
Figure 2. Photomicrographs of germinating spores of stem smut fungi: A, B, *Ustilago spegazzinii*, from *Stipa viridula*; C, *U. nummularia*, from *Stipa comata*; D, *Ibid.*, from *Oryzopsis hymenoides*; E-I, *U. wiliamsii*: E and I, from *Stipa speciosa*, F, from *Stipa cernua*, G & H, from *Oryzopsis hymenoides*; J-M, *U. jacksonii*, from *Stipa lettermani*. X approx. 500.

Stipa robusta Scribn. (*S.* vaseyii) N. Mex.

Stipa viridula Trin. N. Dak., S. Dak., Mont.

3a. USTILAGO SPEGAZZINII var. AGRESTIS (Syd.) G. W. Fisch. and Hirsch.. Mycologia 37: 1945.

Ustilago hypodytes Auct.

Differing from the species as follows: Spores dark brown, usually smooth but under oil immersion sometimes appearing very finely papillose; crests rather inconspicuous, sometimes appearing as lacerated apical thickenings, sub-hyaline to concolorous with the spore.

On: *Stipa californica* Merr. and Davy   Calif.
Stipa occidentalis Thurb.   Calif.
Stipa mucronata (S. setigera)   Mexico
Stipa spartea Ill.
Stipa pulchra Hitchc.   Calif.
Stipa viridula   N. Dak.

Fischer and Hirschhorn (4) have recently demonstrated the confused relationship of *Ustilago spegazzinii* and the var. *agrestis* to *U. hypodytes, U. stipae, U. bromi-erecti,* and *U. agrestis.*

Spore germination has been described by Fischer and Hirschhorn (l.c.). After 24 hrs. or more a single germ tube emerges, elongates, and usually soon becames differentiated more or less into a 3-4 celled promycelium. These cells, however, have not been observed to produce primary sporidia, but, instead, long slender branches. These elongate and re-branch to initiate a mycelium, which soon begins to bear chains of aerial sproidia. Fig. 2, A & B.

4. USTILAGO WILLIAMSII (Griff.) Lavrov Trav. Inst. Sci. Biol. Univ. Tomsk 2: 22. 1936.
Ustilago hypodytes Auct.
Sorosporium williamsii Griff. Bull. Torr. Bot. Club 29: 290-301. 1902.
Ustilago appendiculata Speg. Myc. Arg. en Ann. Mus. Nat. de Buenos Aires. Ser. 3, 12: 288. 1909.
Tranzchiella othophora Lavrov. Trav. Inst. Sci. Biol. Univ. Tomsk 2: 29. 1936.

Sori surrounding the upper internodes, often involving also remnants of the aborted inflorescence, dark-brown to black, naked except for enveloping leaf sheaths; spores globose to sub-globose, provided with an epispore that is smooth, but deeply cracked into large pieces, often appearing as bipolar ears or appendages, dark olivaceous-brown, $7\text{-}10\mu$ in diameter. Fig. 1, C & E; fig. 4, B; fig. 6, D.

On: *Oryzopsis bloomeri* (Boland.) Ricker. Wash.
Oryzopsis hymenoides   Mont., Wyo.
Stipa californica   Calif.

Figure 3. A, *Ustilago minima*, on *Stipa neomexicana*. Note persistent membrane around sori; B. *U. nummularia*, on *Oryzopsis hymenoides;* Approx. nat. size.

Stipa comata Ore., Mont.
Stipa cernua Stebbins and Love   Calif.
Stipa coronata Thurb.   Calif.
Stipa lettermani Wyo.
Stipa occidentalis   Calif., Ore.
Stipa richardsoni Link   Mont., Wyo.
Stipa speciosa Trin. and Rupr.   Calif.
Stipa viridula   Mont.
Stipa thurberiana Piper   Wash.

Many collections of stem smut on *Oryzopsis* and *Stipa* spp. are deposited in the herbaria as *"Ustilago hypodytes,"* but belong to *U. williamsii*.   The larger spores, the cracked exospore, and especially the characteristic appendages make this stem smut species distinct from *U. spegazzinii* var. *agrestis*.   Some collections have more distinctly appendaged spores than others.   In fact occasional collections are encountered in which only the cracked exospore and an occasional appendaged spore identify the species (fig. 1, C).

Germination of the spores takes place rapidly, beginning in 4-6 hours.   On dextrose-malt extract-peptone agar a slender germ tube emerges from one or the other of the appendaged areas and soon develops usually three cross-walls.   From each of the resulting four cells a sporidium or a branch arises, more often the latter (fig. 2, E-G, I).   That these cells of the pro-mycelium represent different sexes seems probable from the fact that fusions between these cells are frequently observed, usually by means of a fusion tube, such as is seen connecting the two proximal cells in fig. 2, H.   The branches of the promycelium rapidly develop more branches, and a vigorous mycelium is thus started.   Very early in the development of this mycelium short, erect hyphae make their appearance and on these are borne short chains of aerial sporidia in great abundance.   These aerial sporidia appear to be identical with such primary sporidia as may be borne on the promycelium.

5. USTILAGO JACKSONII Zundel and Dunlap. North American Flora 7(14) : 982.   1939.

Sori surrounding the upper internodes and more or less consuming the aborted inflorescence, covered only by the enveloping leaf sheaths; spores olivaceous-brown to dark-brown, often quite irregular in shape, globose to ovate, verruculose, mostly 10-12μ in diameter, but often 14μ in length. Fig. 1, F; fig. 5, B; fig. 6, E.

On: *Stipa lettermani* Utah, Colo.

This is the rarest of the stem smuts attacking *Stipa* and *Oryzopsis* in North America. According to Zundel (6), who only recently described the species, it was first collected in 1921, in Colorado.

Only one viable collection[5] of *Ustilago jacksonii* was available and the following observations of spore germination in this species is based on this one collection. At room temperature, spores sown on dextrose-malt extract peptone agar showed no signs of germination for three days, after which approximately 5% of the spores were observed in various stages of germination. One end of the spore begins to protrude, and from this there emerges a short thick germ tube which soon begins to branch and re-branch (fig. 2, J & K). On some germinating spores the germ tube resembles a promycelium, even to the extent of bearing sporidia (fig. 2, L). The process is a slow one compared with the rapidity of germination and subsequent development of *Ustilago williamsii*. Approximately three days are required to reach the extent of development seen in fig. 2, M, in addition to the time required for germination to begin. Advanced states of germination and the development of mycelium have not been observed, due to invasions by contaminating molds which soon over-grow the slowly developing germ tubes and mycelia of the smut fungus.

6. UROCYSTIS FRASERII Clint. & Zundel. N. Amer. Flora 7(14): 1018. 1939.

Sorosporium granulosum Ell. & Tracy Jour. Myc. 6:77. 1890.

Sori more or less surrounding the upper internodes, giving the appearance of a stem smut, but actually composed of numerous more or less confluent linear sori running up into and involving the rachis, surrounded when young by a membrane composed of the host epidermis, the whole elongating from the enveloping leaf sheath as a more or less contorted mass; spore balls very firm, opaque, brown to dark brown, 35-70μ in diameter, sterile cells very irregular, smooth, with walls quite thick in places, as dark as or darker than the spores, chiefly 5-10μ in diameter or 4-6 x 5-14μ; spores globose to subglobose, rather thin-walled, light brown, 8-20 or more per ball, smooth, 14-17 x 17-22μ. Fig. 5, A; fig. 6, F.

On: *Stipa clandestina* Hackel Coahuila, Mexico
Stipa comata Colo., Mont., Sask., Wyo.
Stipa spartea Nebr.
Stipa viridula Colo.

[5] On *Stipa lettermani*. Monte Cristo Mt., Rich Co., Utah. 8-17-41 leg. W. R. Rader, fid. G. W. Fischer, No. 209, Bur. Plant Ind. Myc. Coll. No. 85065.

Figure 4. A, *Ustilago spegazzinii,* on *Stipa viridula;* B, *U. williamsii,* on *Stipa speciosa.* Approx. nat. size.

The presence of two distinctly different kinds of cells in the spore balls excludes this smut from the genus *Sorosporium*, where it was originally placed. Repeated attempts to observe germination of the spores have been unsuccessful except for one germinating spore among thousands of spore balls, spores and sterile cells on an agar plate. This one germinating spore appeared similar to the large cells here considered as the spores and germination was definitely of the *Ustilago* type. However, no other such germinating spores were found on the same agar plate, and previous and subsequent attempts have failed to substantiate the observation. If future studies should prove that spores of this smut fungus germinate such as to place the species in the *Ustilaginaceae* then it probably would become the type species of a new genus, one which would be the counterpart of *Urocystis* in the *Tillitiaceae*. In the meantime, it must be admitted that of existing genera the fungus most closely resembles *Urocystis*. Transferring this smut to the genus *Urocystis* should result in the binomial *U. granulosa* but this name is already occupied, belonging to a distinctly different and rare smut in the spikelets of *Stipa comata,* described by Clinton (2).

Zundel (6) has recently described *Urocystis fraserii,* on *Stipa comata,* from Saskatchewan. After a careful study of type material of this species I am convinced that it is identical with the stem smut under discussion and as long as this smut is considered to be a *Urocystis,* then by priority Zundel's binomial should apply to it. · Apparently Zundel did not recognize the identity of *U. fraserii* with *Sorosporium granulosum,* for each is treated independently in the same publication (6).

COMPARATIVE PATHOLOGICAL HISTOLOGY OF THE STEM SMUTS OF STIPA AND ORYZOPSIS

The apparent superficial nature of the stem smuts has long been the subject of interesting conjecture as to the pathological histology of the host plants. A casual examination of the stems of *Stipa* and *Oryzopsis* affected with these smuts would suggest that the underlying tissues of the host were entirely normal, even including the epidermis. One wonders, therefore, about the nature and extent of the parasitism in these smut diseases. A thorough study of this problem should contribute some valuable data of a fundamental nature. In the present work the parasitism of the fungi and the pathological histology of the hosts have been included in only a very preliminary fashion. Por-
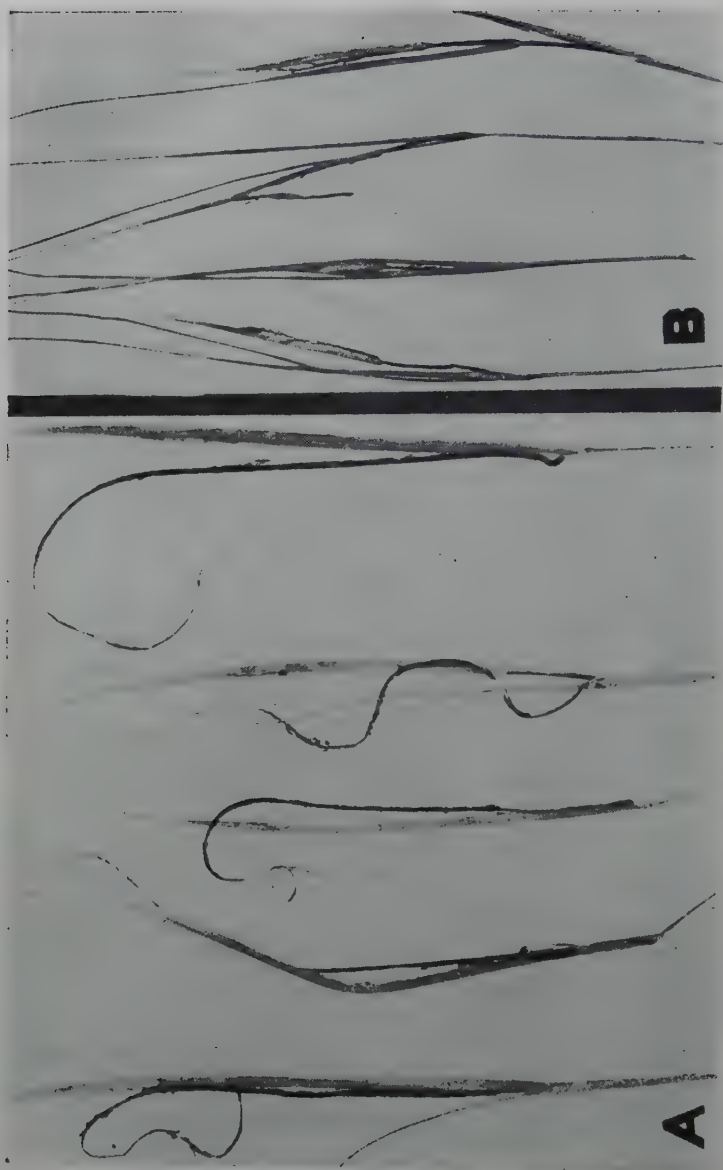
Figure 5. A, *Urocystis fraserii*. on *Stipa comata*; B, *Ustilago jacksonii*, on *Stipa lettermani*. Slightly reduced.

tions of culms of *Stipa* and *Oryzopsis* affected with stem smuts caused by the six species treated above were carried through the paraffin infiltration and embedding process, and sectioned with a rotary microtome. The sections were stained with Thionin and Orange G.

The comparative microscopic appearance of six stem smuts of *Stipa* and *Oryzopsis* is shown in Fig. 6. In all except *Urocystis fraserii* and *Ustilago minima*, the smut appears to be entirely superficial. In the case of *Ustilago nummularia, U spegazzinii, U. williamsii,* and *U. jacksonii* the stem tissues seem to be quite intact. The sections of *O. hymenoides* parasitized by *U. minima* indicate destruction of the epidermis. Finally, it is seen that the parasitism of *Urocystis fraserii* is such that the fungus develops beneath the epidermis, apparently destroying the chlorophyll parenchyma cells, and even some of the mechanical tissue.

Hirschhorn (5) describes the presence of a stroma between the chlamydospore mass and the host epidermis in the case of some of these stem smuts on *Stipa* in Argentina, and states that this character is quite variable according to host species and locality. It may be of some significance that in the present studies no trace of such a stroma was found in any of the six smut species. It is possible that reports of a stroma by other investigators were based on studies of younger sori, in which the superficial mycelium had not entirely converted into a spore mass. It has long been known that spore formation in at least some of the stem smut fungi is centrifugal, and thus the underlying mycelium could easily be interpreted as a spore-bearing stromatic layer. It can scarcely be considered as such a specialized tissue, however, if the layer itself ultimately becomes part of the spore mass. Obviously some careful investigations are needed on the ontogeny of the stem smuts, to clarify such fundamental issues.
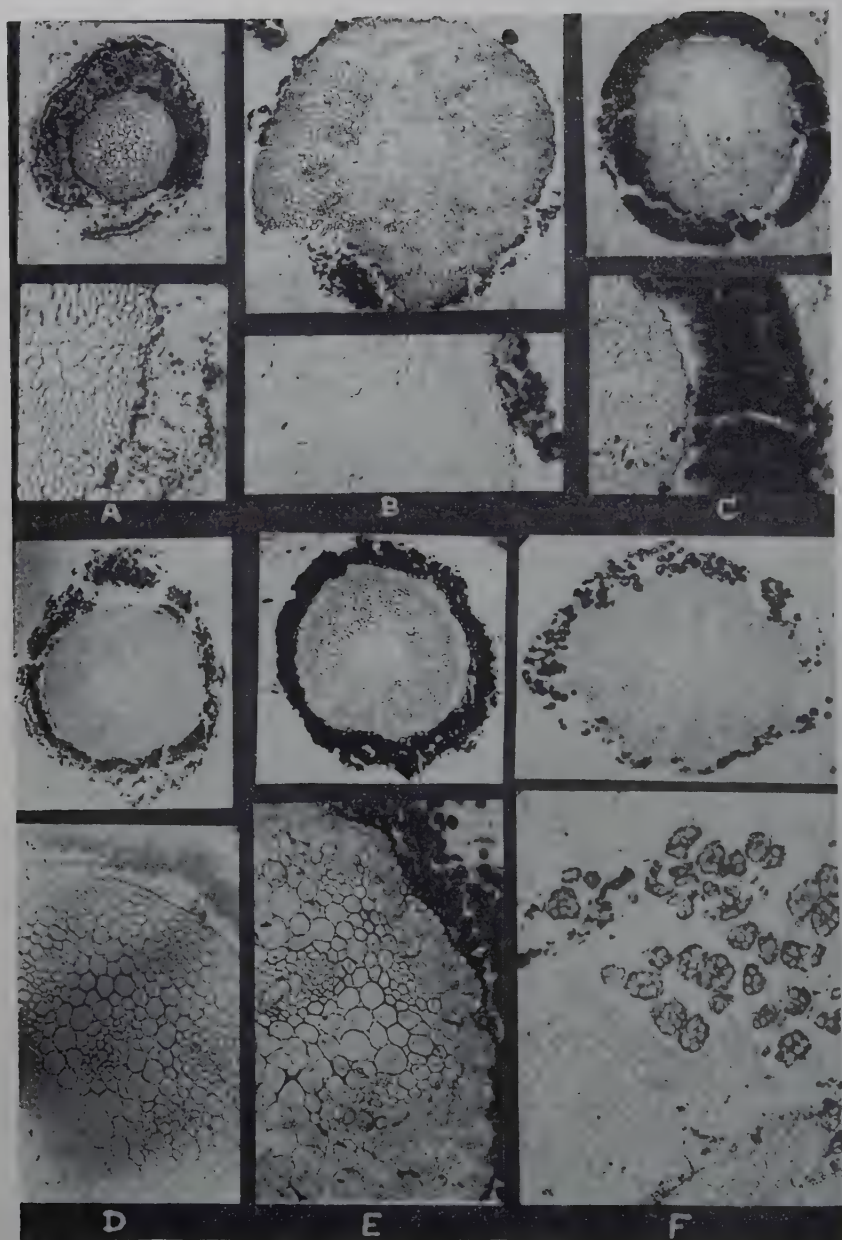
Figure 6. Comparative pathological histology of stems of *Stipa* and *Oryzopsis* affected with stem smuts. Cross sections of the sori and stems (upper row),

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and enlarged portions (lower rows), as follows: A, *Ustilago minima* on *Oryzopsis hymenoides*, note thickness of spore mass and the fungous membrane around same; B, *U. nummularia* on *Stipa comata*; C, *U. spegazzinii* on *Stipa viridula*; D, *U. williamsii*, on *Stipa richardsoni*; E, *U. jacksonii*, on *Stipa lettermani*; F, *Urocystis fraserii*, on *Stipa comata*. Stem sections x approx. 50; enlarged portions x approx. 200.

THE INTERRELATIONSHIP OF NITROGEN SUPPLY AND PHOTOPERIOD ON THE FLOWERING, GROWTH AND STEM ANATOMY OF CERTAIN LONG AND SHORT DAY PLANTS[1]

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INTRODUCTION

The relation of nitrogen to the flowering and fruitfulness of plants has been the subject of extended investigation by many workers. That nitrogen nutrition is intimately related to flower and fruit formation is generally agreed upon, but the various experiments show that apparently the type of responses obtained are not entirely consistent.

Kraus and Kraybill (4) found that an abundant nitrogen supply and ample opportunity for carbohydrate synthesis produced vigorously vegetative and relatively unfruitful tomato plants. By reducing the nitrogen supply somewhat, increased fruitfulness was obtained. Further reduction of the nitrogen supply produced poor vegetative growth and unfruitful plants. When opportunity for carbohydrate synthesis was decreased, vegetation was limited and the plants were also unfruitful. The less vegetative stems were smaller in diameter, possessed greater amounts of xylem, heavier lignification of the wood parenchyma, and a reduced cambial zone as compared to the vigorously vegetative stems.

Some species have been reported either to bloom more quickly under a favorable photoperiod or to flower under an unfavorable photoperiod when the nitrogen supply was limited. Nightingale (6, 7) found that some strains of Salvia, which ordinarily blossom only during a short photoperiod, could be made to flower profusely under long days by limiting the external nitrogen supply and permitting an accumulation of carbohydrates. Borodin (1) reported

that, by limiting nitrogen, she induced barley to head at a day length usually associated with vegetative growth. Knott (3) found that spinach plants grown in sandy loam soil were greatly delayed in the formation of seed stalks when large quantities of sodium nitrate were added to the soil. Roberts and Struckmeyer (8) showed that some plants, as lettuce, will respond sooner to photoperiod under conditions of low nitrogen supply than under conditions of higher nitrogen supply.

On the other hand, Neidle (5) reports that Xanthium, a short day plant, growing under a short photoperiod, bloomed more quickly with an abundant nitrogen supply than with a low nitrogen supply. Those plants given an induction period of seven short days and then grown under long days bloomed also more quickly with an abundant nitrogen supply. More burs were produced by the high nitrogen plants than by the low nitrogen ones under both photoperiods.

Cajlachjan and Lukovnikov (2) found that mineral nutrient supply had no effect in bringing either the long day plant, Pobeda variety of oat, or the short day plant, West China variety of millet, into flower under unfavorable photoperiods. In favorable photoperiods, the flowering of oat was retarded and the flowering of millet was accelerated by abundant amounts of nutrient salts.

The investigation to be reported was planned to ascertain the responses obtained with nitrogen and without nitrogen under long and short photoperiods for both long and short day plants, and to observe whether age and size of the plant and previous induction treatment are influential in altering the response to nitrogen supply. It was also an object of this study to attempt a correlation of the stem anatomy with the flowering and growth response to nitrogen supply and photoperiod.

PROCEDURE

The plants were grown in greenhouse subirrigation gravel cultures in eight, four-foot square boxes. Each box was supplied with a separate nutrient solution tank and pump. The plants were all given nine hours of daylight from 7:30 A.M. to 4:30 P.M. At 4:30 P.M. a heavy rubberized curtain, black on the interior and aluminum coated on the exterior, was pulled over the plants. This was so constructed that all daylight was excluded. The plants in one set of four boxes received a short photoperiod and those in the second set of four boxes

Plate I.

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were given a long photoperiod. The two sets of boxes were separated from each other by a black rubberized curtain.

The plants under the long photoperiod received red radiant energy equivalent to approximately ten foot candles of incandescent lamp irradiance for 15 hours daily to total a 24-hour day. No dark period was given the plants under the long photoperiod. The radiation filters were similar to those reported by Withrow and Withrow (12).

In each of the photoperiod treatments, two boxes, one containing long day plants and one with short day plants, were given the plus nitrogen solution as shown in table I. The second two boxes of each set were given the minus nitrogen solution. The solutions were kept at a pH of 5.5 to 6.5 and were changed weekly.

The plants were seeded in flats. The long day plants were kept under a short photoperiod until placed in the nitrogen boxes or were irradiated as indicated in the tables. The short day plants were given a 24-hour photoperiod made up of nine hours of daylight supplemented with 15 hours of ten foot candles of red irradiance from germination until the beginning of the nitrogen treatments, or as indicated in the tables.

The plant material consisted of two long day species, *Scabiosa atropurpurea*, variety Azure Fairy, and *Spinacia oleracea*, variety Nobel (spinach), and of four short day species including *Tithonia speciosa*, *Soya max*, variety Biloxi (soybean), *Salvia splendens*, variety Fairly Tall, and *Xanthium pennsylvanicum* (cocklebur).

The temperature of the greenhouse was manually maintained at 52 to 55° F. during the night and 62 to 65° F. during the day for most of the experimental period. It was raised to above 70° F. for the 24-hour period during the latter part of the experiment, as indicated in the tables.

Data on the time of formation of macroscopic floral buds, flowering time, height, and fresh and dry weights were taken. The plant

Plate I.

The interrelated effect of the nitrogen and photoperiod treatments on Scabiosa. Plants shown in upper figure received a period of long days previous to the beginning of the nitrogen treatments, with a night temperature of 52 to 55° F. Plants in center received only short photoperiods previous to the beginning of the nitrogen treatments and the indicated photoperiods thereafter. Plants in lower figure show the flowering response occurring under short photoperiods when the night temperature was raised above 70° F. Note earlier flowering in —N condition as compared to +N treatment.

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material was dried for 24 hours in a forced draft oven thermostatically controlled at 100° C.

Transections of the stems were taken at the second elongated internode below the apical bud. Sections of five plants from each treatment were taken for Scabiosa, soybean and Salvia. The sections were killed and fixed in formalin-acetic alcohol, cut in celloidon, and stained with fast green and safranin.

RESULTS

FLOWERING RESPONSES

In no case did the nitrogen treatments induce flower bud formation in an unfavorable photoperiod or prevent it in a favorable photoperiod. However, the time of flowering of some of the species was affected, the effect dependent upon the age and previous radiation treatment. The long day plants exhibited a tendency to flower earlier when the plants were without an external nitrogen supply. The short day plants in the short photoperiods flowered earlier with an abundant nitrogen supply when any difference in flowering time occurred. However, when Tithonia flowered under the long photoperiod, earlier flowering occurred without than with an external nitrogen supply. In all cases, where flower bud formation was observed, the number of floral buds and flowers was greater when the plants were given the plus nitrogen solution than with the minus nitrogen solution.

TABLE I
NUTRIENT SOLUTION FORMULAE

| | CONCENTRATION millimolar | |
SALT	Plus N Solution	Minus N Solution
MgSO$_4$	0.5	0.5
Ca(H$_2$PO$_4$)$_2$	0.5	0.5
KNO$_3$	6.0	—
KCl	—	6.0
Ca(NO$_3$)$_2$	6.0	—
CaSO$_4$	—	6.0

Scabiosa plants flowered only under the long photoperiods when the night temperatures were below 55° F., as indicated in table II and plate I. The plants without nitrogen in the nutrient solution formed flower buds and flowered sooner than did those supplied with nitro-

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gen. This was true whether or not the plants had been in long days previous to the beginning of the nitrogen treatment. When the night temperature was raised above 70° F., the Scabiosa plants receiving a short photoperiod and no nitrogen formed macroscopic flower buds 25 days after the temperature was raised and flowered in 55 days. The plants receiving short photoperiods and an external nitrogen supply formed macroscopic floral buds in 55 days and open flowers in 90 days. When the long photoperiod was begun fairly early in the life of the plant, a longer period of irradiation was required for flower bud formation than was necessary when larger and older plants from the short photoperiod were placed under long days.

Spinach was kept under a short photoperiod until removal to the nitrogen boxes. Plate II shows the variation in flowering response obtained with the different treatments. Floral buds were formed only in the long photoperiod. Plants without nitrogen formed macroscopic buds two weeks sooner than did those supplied with nitrogen. This is similar to the type of response secured by Knott (3).

Plate II.
The interrelated effects of nitrogen and photoperiod treatments on spinach (upper), Tithonia (center), and soybean (lower).

TABLE II

Effect of Nitrogen and Photoperiod Treatments When Applied at Different Ages on *Scabiosa atropurpurea*, variety Azure Fairy

Treatment	No. Days to Bud*	No. Days to Flower*	Av. No. Buds and Flowers Per Plant	Av. No. Branches Per Plant	Av. Ht. cm.	Average Dry Weight Per Plant						Top-Root Ratio	Dry Matter %
						Bud gm.	Leaf gm.	Stem gm.	Top gm.	Root gm.	Total gm.		
Long photoperiod begun 37 days from seeding; transferred to nitrogen boxes 69 days from seeding. Harvested 45 days after transfer to nitrogen boxes; 24 plants per treatment.													
Short Day −N	—	—	1 vegetative bud	—	2	0.01	1.13	0.06	1.20	0.39	1.59	3	10
Short Day +N	—	—	3 vegetative buds	—	4	0.02	1.86	0.13	2.01	0.28	2.29	7	7
Long Day −N	61	108	3 floral buds and flowers	—	55	0.01	0.85	0.80	1.66	0.22	1.88	8	12
Long Day +N	74	121	4 floral buds and flowers	—	38	0.03	1.42	0.60	2.05	0.20	2.25	10	8
Long photoperiod begun 37 days from seeding; transferred to nitrogen boxes 69 days from seeding. Harvested 90 days after transfer to nitrogen boxes; 14 plants per treatment.													
Short Day −N	—	—	—	—	4	—	—	—	2.18	0.87	3.05	3	12
Short Day +N	—	—	—	—	33	—	—	—	16.48	1.63	18.11	10	9
Long Day −N	61	108	4 (56% in open flower)	—	97	—	—	—	3.69	0.44	4.13	8	19
Long Day +N	74	121	16 (19% in open flower)	—	110	—	—	—	31.95	1.48	33.43	22	14
Long photoperiod begun 138 days from seeding; transferred to nitrogen boxes 138 days from seeding. Harvested 70 days after transfer to nitrogen boxes; 10 plants per treatment.													
Long Day −N	19	51	45	29	143	0.65	1.06	12.41	14.12	3.60	17.72	4	11
Long Day +N	32	62	70	71	134	0.42	1.92	17.33	19.67	3.30	22.97	6	9

* From beginning of long photoperiod treatment.

TABLE III

Effect of the Nitrogen and Photoperiod Treatments When Applied at Different Ages on *Tithonia speciosa*.

Treatment	No. Days to Bud*	No. Days to Flower*	Av. No. Buds and Flowers Per Plant	Av. No. Branches Per Plant	Av. Ht. cm.	Average Dry Weight Per Plant Bud gm.	Leaf gm.	Stem gm.	Top gm.	Root gm.	Total gm.	Top-Root Ratio	Dry Matter %
Short photoperiod begun at germination; transferred to nitrogen boxes 56 days from seeding. Harvested 40 days after transfer to nitrogen boxes; 20 plants per treatment.													
Short Day —N	57	91	2 floral buds and flowers	0	41	0.12	0.82	1.07	2.01	0.45	2.46	4	12
Short Day +N	57	92	11 floral buds and flowers	4	69	0.43	2.79	2.22	5.44	0.85	6.29	6	11
Long Day —N	—	—	1 vegetative bud	0	57	0.01	0.98	1.53	2.52	0.37	2.89	7	12
Long Day +N	—	—	4 vegetative buds	1	76	0.02	2.25	2.46	4.73	0.77	5.50	6	8
Short photoperiod begun 32 days from seeding; transferred to nitrogen boxes 32 days from seeding. Harvested 67 days after transfer to nitrogen boxes; 10 plants per treatment.													
Short Day —N	60	—	1 floral bud	0	13	—	—	—	0.66	0.25	0.91	3	12
Short Day +N	27	63	17 floral buds and flowers	9	69	+	—	—	7.62	1.03	8.65	7	10
Long Day —N	—	—	1 vegetative bud	0	26	—	—	—	0.37	0.10	0.47	4	11
Long Day +N	—	—	1 vegetative bud	0	64	—	—	—	5.92	1.04	6.96	6	9
Short photoperiod begun 76 days from seeding; transferred to nitrogen boxes 76 days from seeding. Harvested 58 days after transfer to nitrogen boxes. Temperature raised above 70° F. 17 days after transfer to the nitrogen boxes.													
Short Day —N	17	45	10 floral buds and flowers	—	118	2.06	2.74	6.90	11.70	1.92	13.62	6	16
Short Day +N	17	42	70 floral buds and flowers	—	112	11.90	15.60	25.20	52.70	5.72	58.42	9	15
Long Day —N	33 (16)**	—	15 vegetative buds (4 floral buds on 3 plants)	—	73	0.11	3.47	4.70	8.28	2.15	10.43	4	12
Long Day +N	51 (34)**	—	28 vegetative buds (3 floral buds on 3 plants)	—	123	0.27	15.22	19.73	35.22	4.00	39.22	9	10

* From beginning of short day treatment. ** From the time the temperature was raised.

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Tithonia (table III, plate II) flowered only in short days when the night temperatures were in the range of 52 to 55° F., but flower buds were formed in both photoperiods when the night temperatures were above 70° F. However, only a few plants formed flower buds under the long photoperiod. When the plants received a period of short days before the nitrogen treatments were begun, the time of flower bud opening was not affected although the number of flower buds produced was greater with nitrogen than without. When the photoperiod variables and the nitrogen treatments were begun at the same time, using small young plants, the plants with nitrogen formed macroscopic flower buds much sooner than did those without nitrogen. The plants under the short day minus nitrogen condition failed to open their flower buds. However, if the plants were allowed to become quite large under a long photoperiod and then were transferred to the nitrogen treatments under short and long photoperiods, there was no difference in the time of appearance of macroscopic buds in the short days. When the plants treated with long photoperiods formed floral buds under the high night temperatures, those without nitrogen formed floral buds considerably ahead of those supplied with abundant nitrogen.

The soybean plants (table IV and plate II) were kept under a long photoperiod until transferred to the nitrogen boxes and, therefore, received no previous floral induction period. Flower bud formation and flowering occurred in the short photoperiods at the same time without reference to the nitrogen supply. No flower bud formation occurred under the long photoperiods.

Salvia (table V and plate III), which received no induction period previous to transfer to the nitrogen boxes, formed macroscopic floral buds and bloomed a few days sooner with an external nitrogen supply than without. Flowering took place only in the short photoperiod. The response of Salvia was not the same as that secured by Nightingale (6, 7), who reported flowering in a long photoperiod and no flowering in a short photoperiod when the external nitrogen supply was limited. In the present experiment, flowering was not very vigorous in the short photoperiod when the plants were grown with the minus nitrogen solution, only one floral spike per plant being formed as compared with an average of 53 for those plants given abundant nitrogen.

TABLE IV

Effect of the Nitrogen and Photoperiod Treatments on *Soya Max*, variety Biloxi

Short photoperiod begun and transfer to nitrogen boxes 20 days from seeding. Harvested 25 days after transfer to nitrogen boxes; 10 plants per treatment. Temperature: 70° F. and above.

Treatment	No. Days to Bud*	No. Days to Flower*	Av. No. Buds and Flowers Per Plant	Av. No. Leaves Per Plant	Av. No. Nodules Per Plant	Av. Ht. cm.	Average Dry Weight Per Plant					Top-Root Ratio	Dry Matter %
							Bud & Leaf gm.	Stem gm.	Top gm.	Root gm.	Total gm.		
Short Day —N	10	22	25 floral	4	0	26	0.60	0.56	1.16	0.48	1.64	2	17
Short Day +N	10	23	35 floral	12	0	35	2.61	1.52	4.13	0.46	4.59	9	13
Long Day —N	—	—	5 vegetative	4	17	31	0.54	0.62	1.16	0.41	1.57	3	16
Long Day +N	—	—	10 vegetative	12	0	49	3.12	2.33	5.45	0.47	5.91	12	15

* From beginning of short day treatment.

TABLE V

Effect of the Nitrogen and Photoperiod Treatments on *Salvia splendens*, variety Fairly Tall.

Short photoperiod and nitrogen treatment begun 73 days from seeding. Harvested 56 days after transfer to the nitrogen boxes; 10 plants per treatment. Temperature: 70° F. and above for 30 days previous to harvest.

Treatment	No. Days to Bud*	No. Days to Flower*	Av. No. Buds and Flowers Per Plant	Av. No. Branches Per Plant	Av. Ht. cm.	Average Dry Weight Per Plant						Top-Root Ratio	Dry Matter %	
						Bud gm.	Leaf gm.	Stem gm.	Top gm.	Root gm.	Total gm.			
Short Day —N	31	52	1	2	23	0.03	0.75	0.69	1.47	0.79	2.26	2	Leaf	9
													Stem	16
													Root	7
													Total	9
Short Day +N	27	45	53	24	82	1.11	16.57	12.80	30.48	4.66	35.14	7*	Leaf	13
													Stem	11
													Root	7
													Total	11
Long Day —N	—	—	—	0	32	—	0.99	1.09	2.08	0.88	2.96	2	Leaf	8
													Stem	16
													Root	8
													Total	10
Long Day +N	—	—	—	14	99	—	9.26	8.50	17.76	3.65	21.41	5	Leaf	15
													Stem	12
													Root	8
													Total	12

* From beginning of short day treatment.

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Plate III.

The interrelated effect of nitrogen and photoperiod treatments on Salvia (upper), and Xanthium (lower), showing the small non-branching growth under —N treatments.

TABLE VI

Effect of the Nitrogen and Photoperiod Treatments on *Xanthium pennsylvanicum*

Short photoperiod and nitrogen treatments begun 35 days from seeding. Harvested 60 days from beginning of treatments; 10 plants per treatment. Temperature: 70° F. and above for 30 days previous to harvest.

Treatment	No. Days to Bud*	Av. No. Fruits Per Plant	Av. Ht. cm.	Average Dry Weight Per Plant						Top-Root Ratio	Dry Matter %
				Bud gm.	Leaf gm.	Stem gm.	Top gm.	Root gm.	Total gm.		
Short Day −N	10	22	25	1.49	0.99	0.64	3.12	0.46	3.58	7	21
Short Day +N	10	82	49	4.90	6.30	2.59	13.79	1.08	14.87	13	15
Long Day −N	—	—	40	—	1.75	2.49	4.26	0.85	5.11	5	20
Long Day +N	—	—	93	—	11.50	8.46	19.96	2.73	22.69	7	13

*From beginning of short day treatment.
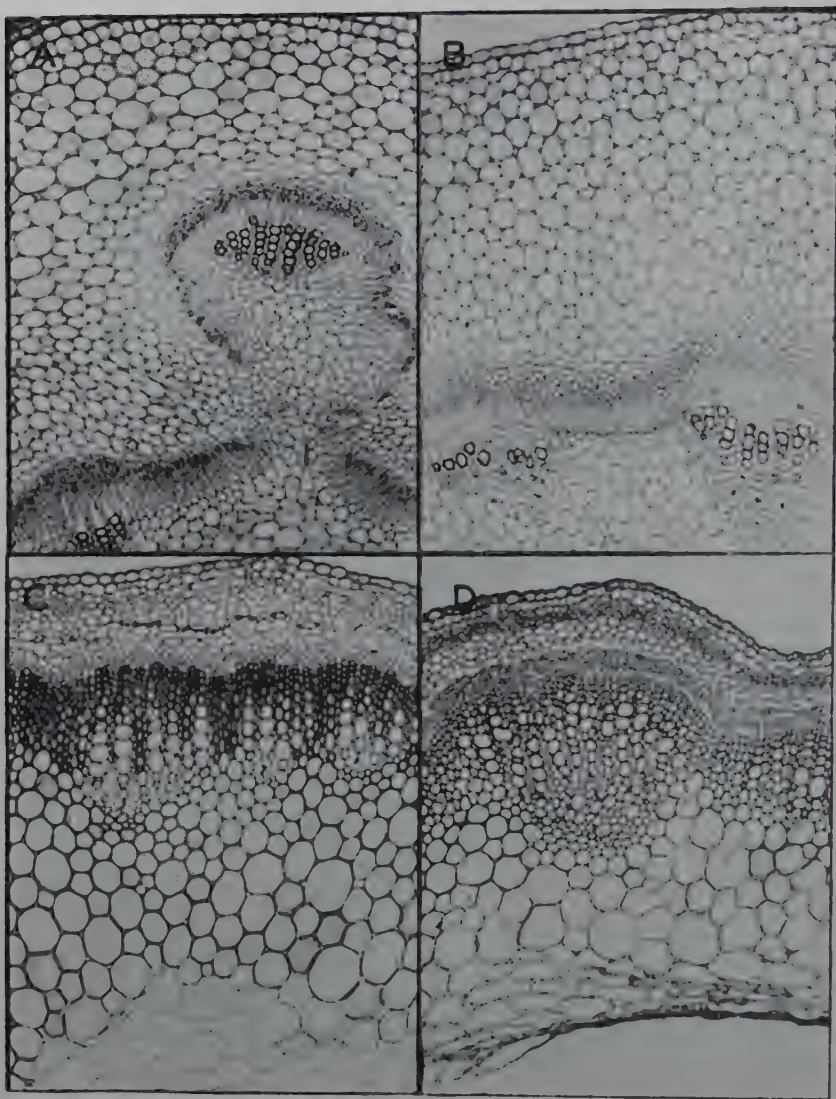
Plate IV.

Transections of the stem of Scabiosa taken 90 days from the beginning of the nitrogen treatments, showing effect of photoperiod and nitrogen on cell wall lignification, cell size, proportion of xylem to phloem, and tissue maturation.

A. Short day —N, vegetative stem shows leaf traces and small bundles with a large number of undifferentiated cells. Av. diam.: 4.0 mm.

Xanthium (table VI and plate III) likewise received no floral induction period previous to the beginning of the nitrogen treatments, but, unlike Salvia, no difference could be observed in the time of formation of macroscopic floral buds under the two short photoperiod treatments. The plants flowered and fruited only under the short photoperiod. Although the nitrogen supply did not affect the time of flower bud formation, the average number of fruits was much greater when the plants were given an abundant nitrogen supply than when they were deprived of external nitrogen. The fruiting responses were similar to those found by Neidle (5), although Neidle reported that in her studies Xanthium blossomed more quickly with abundant nitrogen supply than with a limited supply.

Vegetative Responses

The nitrogen supply did not materially affect the type of weight response to the plant to photoperiod for Tithonia (table III) where the total dry weights were usually greater in the short photoperiod, or for Scabiosa (table II) and Xanthium (table VI) where the total dry weights were usually greater in the long photoperiod. The type of weight response of Salvia (table V) and soybean (table IV) was somewhat affected by nitrogen supply. With a high nitrogen level, Salvia was heavier in the short photoperiod and soybean was heavier in the long photoperiod, but with a limitation of nitrogen supply, the weights in long and short days were quite similar, although a slight reversal of response occurred in both species. Under either photoperiod, all the plants furnished with a high level of nitrogen were heavier than those given the minus nitrogen solution, the weight difference usually holding for all parts of the plant.

The nitrogen level did not affect the type of response to photoperiod in ratio of tops to roots in the case of Scabiosa and soybean,

B.   Short day +N, vegetative stem has larger bundles than those shown in A and somewhat thinner cell walls. Av. diam.: 7.0 mm.

C.   Long day —N, flowering stem exhibits complete maturation of all vascular tissue, heavy lignification of xylem and pith cells, and a larger proportion of xylem to phloem than shown in the vegetative stems (A, B). Av. diam.: 4.2 mm.

D.   Long day +N, flowering stem shows complete maturation of all vascular cells, and a larger proportion of xylem to phloem than in the vegetative stems (A, B). There is less lignification than in the —N condition. Av. diam: 5.5 mm.

which had greater ratios in the long photoperiods, or for Xanthium which had greater ratios in the short photoperiods. Under either photoperiod, the ratios were always greater where the plants received the high nitrogen level. Salvia, on the other hand, gave a greater ratio in the short photoperiod if abundant nitrogen were available, but with the minus nitrogen solution there was no difference in the ratios. Tithonia showed little difference in top-root ratios in relation to photoperiod at high nitrogen levels, but with the minus nitrogen solution, the ratios appeared to be dependent upon the age of the plants and the pre-radiation treatment.

Nitrogen supply generally had no effect on the percentage of dry matter in relation to photoperiod, although in either photoperiod the plants with the minus nitrogen solution had a higher percentage than those grown at high nitrogen levels. The flowering plants had a higher percentage than the vegetative plants, except soybean which gave a higher percentage in the vegetative plant at high nitrogen levels. Salvia gave results which were an exception to these general findings due chiefly to the higher percentage of dry matter found in the leaves of the plus nitrogen plants as compared to the minus nitrogen ones and in the leaves of the vegetative as compared to the flowering plants.

Usually the nitrogen supply did not alter the type of height response to photoperiod, those plants given the long photoperiod generally being taller than those in the short. The plants given the high nitrogen level were taller than those given the minus nitrogen condition under either photoperiod, except where much earlier flowering occurred when the nitrogen supply was limited as with Scabiosa in the long photoperiod, or where the Tithonia plants were quite large on transfer to the nitrogen and photoperiod variables.

For the short day plants, the number of branches was greater in the short photoperiod, with more branches in the plus nitrogen than in the minus. Scabiosa in the long photoperiod also produced more branches with the plus nitrogen solution.

The soybean plants in both photoperiods averaged about three times as many leaves remaining on the plants at harvest when they received a high nitrogen level as when they were supplied with the minus nitrogen solution. During the 25 days in the nitrogen boxes, no nodules were developed on any of the soybean plants except on those receiving the long photoperiod and the minus nitrogen solution.

Plate IV presents transections of Scabiosa stems taken from plants grown under the different treatments. The nitrogen supply altered the type of anatomical response to photoperiod in the short photoperiod, although it did not do so in the long photoperiod. Sections of the rosette Scabiosa plants grown in the short photoperiod without nitrogen show a stem with numerous large leaf traces and show sections of the leaf petioles surrounding the stem section. The stems of the plants under the other conditions were elongated and no leaf traces or petiole bases were found in the internodal area selected for sectioning. Bundles of the minus nitrogen plants from the short photoperiod were smaller and consisted of smaller cells than those of the plus nitrogen plants. Parenchyma and non-differentiated vascular cells of the minus nitrogen stem were rich in protoplasm, stained densely. In the plus nitrogen stem from the short photoperiod there appeared to be more differentiation and maturation of the vascular tissue than in the minus nitrogen stem.

In the long photoperiod, nitrogen supply had little effect on the type of anatomical response secured. Without nitrogen, the stems were smaller in diameter and the xylem and pith cells were more heavily lignified than at high nitrogen levels. Flowering stems from the long photoperiods had smaller epidermal and hypodermal cells with heavier walls, a much reduced cortical zone, more heavily lignified xylem and larger and more heavily lignified pith cells than the vegetative stems from the short photoperiods. Early formed xylem cells were chiefly vessels, but later formed xylem consisted principally of fibers and lignified parenchyma cells. All cells in the xylem and phloem were differentiated and mature at the time of sectioning. A much larger proportion of xylem to phloem occurred in the flowering stem than in the vegetative stem.

Nitrogen supply did not alter the type of anatomical response to photoperiod given by soybean stems (plate V), although under either photoperiod, heavier cell walls, especially in the xylem and pericycle, and smaller cells were present in plants grown without nitrogen than in those grown with a high nitrogen level. Flowering stems from the short photoperiods had smaller cells and bundles. More lignification and heavier cell walls were present in the minus nitrogen flowering stems than in the minus nitrogen vegetative stems. There were more matured xylem cells in the flowering stems than in the vegeta-

Plate V.

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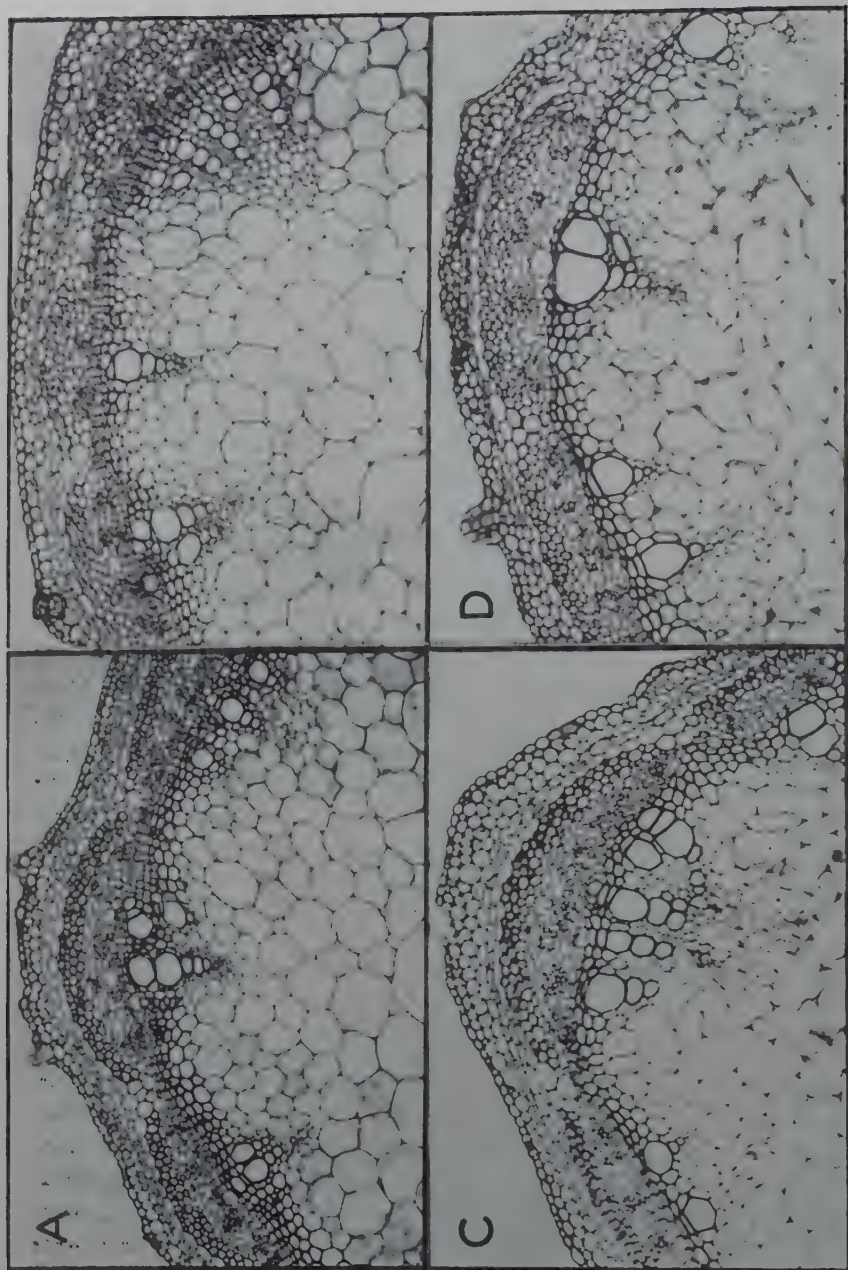
tive ones, but the width of the xylem zone was smaller due to the smaller size of the cells. Thus, the proportionate size of xylem to phloem was greater in the vegetative stems than in the flowering stems, although the proportionate number of matured xylem cells was less.

Nitrogen supply affected the anatomical response of Salvia to photoperiod (plate VI) under both short and long photoperiods to a greater degree than that of either Scabiosa or soybean, with the greatest influence in the short photoperiod. Salvia plants grown in the short photoperiod with the minus nitrogen solution were weakly flowering and small in size, while those grown with abundant nitrogen were tall, large plants and were vigorously flowering. The pericycle and xylem of the plus nitrogen stems under the short photoperiod were more heavily lignified than were those from the minus nitrogen stems and, except for the pith, the cells were smaller in size. Only in the epidermis and collenchyma did the minus nitrogen stems show heavier cell walls. In plus nitrogen plants, the xylem consisted chiefly of fibers and lignified wood parenchyma with vessels fairly numerous in the early formed tissue and less numerous in the later formed xylem, while in the minus nitrogen plants there were more numerous vessels, arranged radially, and fewer fibers.

Under long photoperiods, bundles and cells were much larger in size than in the short day, and, except for the vessels, there was much less lignification generally. However, there were some ligni-

Plate V.

Transections of the stem of Biloxi soybean taken 25 days from the beginning of the nitrogen and photoperiod variables, showing the effect of these variables on cell wall lignification, cell size, and width of cambial zone.

A. Short day —N, flowering stem shows heavy lignification of the xylem and pericycle. Av. diam.: 2.0 mm.

B. Short day +N, flowering stem has less lignification than in A. Av. diam.: 2.3 mm.

C. Long day —N, vegetative stem exhibits larger cells than in the flowering stems (A, B), and fewer xylem cells than in A. Fairly heavy lignification of the pericycle is present. Av. diam.: 2.0 mm.

D. Long day +N, vegetative stem has larger cells than in the other conditions, especially the vessels. There are fewer xylem cells than in B, and lignification of the pericycle is not so heavy as in the —N stem (C). Av. Diam.: 2.0 mm.
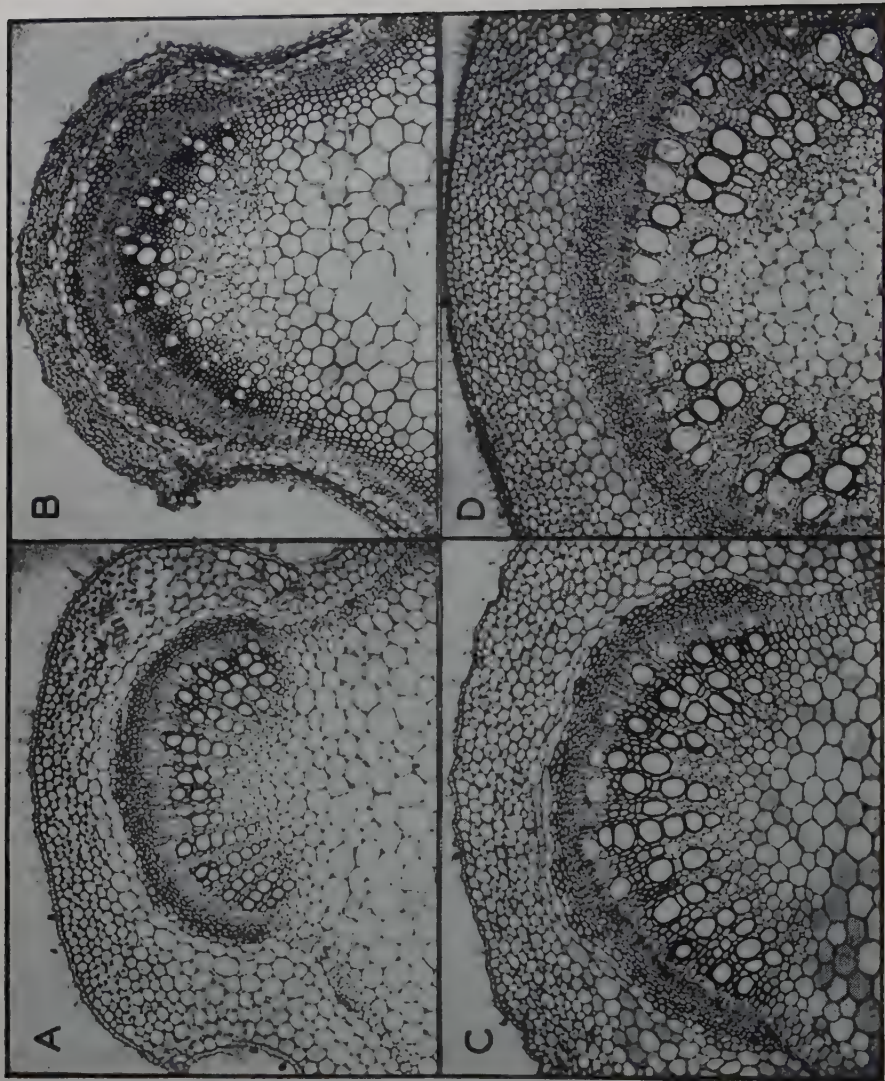
Plate VI.

Transections of the stem of Salvia taken 56 days from the beginning of the nitrogen and photoperiod variables showing effect of these variables on cell wall lignification, cell size, and tissue maturation.

A. Short day —N, flowering stem has radially arranged vessels and wood parenchyma and pericycle cells are not very heavily lignified. Av. diam.: 2.5 mm.

fied pericyclic fibers in the minus nitrogen stems from the long photoperiod, whereas in the minus nitrogen stem from the short photoperiod, the fibers were not so heavily lignified. Vessels were numerous in both the plus and minus nitrogen treatments, with many unlignified vessels present in the later formed tissue. There was a considerably larger amount of xylem parenchyma in the plus nitrogen than in the minus nitrogen stem. However, there was no very extensive lignification of these cells as in the plus nitrogen treatment in the short photoperiod. The vessels were smaller and the wood parenchyma had heavier walls in the minus nitrogen condition.

The same situation held with regard to the proportion of xylem to phloem in the flowering and vegetative stems as was true in soybean, *i. e.*, a proportionately wider band of xylem in relation to phloem was present in the vegetative stem due to the large cell size. However, there were proportionately fewer matured xylem cells than in the flowering stem. The cambial zone was reduced in size in the flowering stem as compared to the vegetative stem.

DISCUSSION OF RESULTS

In these experiments, the external supply of nitrogen was not a decisive factor, as were photoperiod and temperature, in determining the ultimate flowering or vegetativeness of the plant. However, the time of flower bud appearance and flowering was considerably affected by the nitrogen treatment in some species. The abundance of flowers and laterals appearing when the plants were supplied with nitrogen may be largely associated with the vigorous vegetative development prevalent with this treatment as contrasted with the poor vegetative development occurring with the minus nitrogen solution. This more

B. Short day $+N$, vigorously flowering stem has heavy lignification of the pericycle and wood parenchyma cell walls. The vessels are more scattered in arrangement than in A. Note the prevalence of wood fibers. Av. diam.: 3.3 mm.

C. Long day $-N$, vegetative stem exhibits some lignification in the pericycle and wood parenchyma. The cells are larger than in A and there is a wider band of undifferentiated cells than in the flowering stems (A,B). Av. diam.: 3.5 mm.

D. Long day $+N$, vegetative stem has larger vessels than in the other conditions. The pericycle and wood parenchyma cells are not heavily lignified as in B. There is a wider band of undifferentiated tissue here than in the flowering stems (A,B). Av. diam.: 4.5 mm.

vigorous growth was reflected in the greatly increased dry weights of the plants grown with nitrogen and in their increased height.

The top-root ratio data indicates that the plants, for the most part, were able to form proportionately larger tops as compared to roots under that photoperiod which brought about flowering as compared to that photoperiod under which the plants remained vegetative. Nitrogen supply did not usually alter the direction of this response although under either photoperiod, there were proportionately larger tops as compared to roots at high nitrogen levels than when the nitrogen supply was limited. These greater top-root ratios were due chiefly to increased weight of tops and not to decreased weight of roots.

Nightingale and others (7, 5) have pointed out that when the external nitrogen supply is limited, an abundance of stored carbohydrates results. The stem sections in this series of experiments show that there was a deposition of much carbohydrate material in the cell walls of the stem as lignin and cellulose when the plants were flowering or were deprived of nitrogen. The percentage of dry matter, with one exception, was also greater under these conditions. The greater lignification of the plus nitrogen Salvia plants under the short photoperiod is probably directly related to the more vigorous flowering of these plants. The greater percentage of dry matter resulting from the plus nitrogen treatment of Salvia was due to the greater percentage of dry matter in the leaves as compared to the minus nitrogen plants.

The flowering stems, as compared with vegetative stems, were smaller in diameter in some cases and larger in others. They possessed a proportionately greater number of matured xylem cells as compared with phloem cells. There was heavy lignification of wood parenchyma and, in some cases, there was a reduced zone of undifferentiated cells. They resembled, in many respects, the weakly vegetative tomato stems described by Kraus and Kraybill (4). The present investigation substantiates the findings of Wilton and Roberts (11), Roberts and Struckmeyer (8, 9), and Struckmeyer (10), with regard to the proportionate number of xylem to phloem cells matured in the flowering as compared to the vegetative stem. The reduced cambial zone found in the flowering stems is in accord with results previously found by Roberts and his coworkers.

CONCLUSIONS

1. External nitrogen supply is not a determining factor in floral initiation as are photoperiod and temperature.

2. External nitrogen supply does alter the time of appearance of macroscopic buds and flowering in some species, especially if small vegetative plants without large quantities of reserve nitrogen are used.

3. The direction of the photoperiod effect on total dry weight, percentage of dry matter, top-root ratio or height response usually was not altered by the amount of nitrogen supplied to the plants.

4. Plants given an abundant nitrogen supply were heavier, taller and had a lower percentage of dry matter than those to which the supply was limited.

5. Plants in a long photoperiod were usually taller than those given the same nitrogen supply in a short photoperiod.

6. Flowering plants usually had a higher percentage of dry matter, higher top-root ratio, and, in many cases, greater total dry weight than vegetative plants.

7. Limitation of nitrogen supply markedly altered the anatomical response of the stems. When nitrogen was limited, a reduction in cell size and an increase in cell wall thickness, with greater lignification, occurred in the long photoperiod in the species investigated, whether the plants were in the flowering or vegetative condition. In the short photoperiod, the results were variable. Salvia plants with an abundant nitrogen supply had heavier walled and smaller cells, while the reverse was true in soybean.

8. A smaller proportion of phloem to xylem cells usually was present in the flowering stems as compared to the vegetative stems. There was also a greater proportion of undifferentiated cells in vegetative stems than in flowering ones.

ACKNOWLEDGMENT

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A STUDY OF POLLEN GRAINS OF THIRTY-TWO SPECIES OF GRASSES*

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The study of fossil pollens from bogs and lake sediments shows that sometimes the percentage of grasses runs quite high. The presence of large amounts of grass pollens has usually been interpreted, often without justification, as proof of prairie invasion. It is certainly necessary to determine the genera of grasses which contributed the pollen before such a conclusion can be made. Keller (5) attempted this in his work on three Indiana bogs. Careful examination and measurements of the grass pollens found and comparison with size frequency of pollens from modern grasses forced him to the conclusion that the predominating pollen present in the bogs was that of *Calamagrostis canadensis* and not of prairie species. For that reason it has no diagnostic value as an indicator of a xerothermic period in northern Indiana.

In the present study an attempt is made to find some means of differentiating between various genera of grasses which are representative of ecological factors, with special emphasis on diagnostic differences between groups of typical prairie and typical aquatic grasses.

GENERAL CHARACTERISTICS OF GRASS POLLENS

Wodehouse (8) states that the pollen grains of the Gramineae are remarkably uniform throughout. The shape may be spheroidal, ovoidal, or ellipsoidal. The size range is from 32 microns to a little over 100 microns.

Erdtman (3), in summarizing the work of Firbas, divides grass pollens into two groups according to size, viz. the *wild grass type,* which ranges in size from 25 to 35 microns (the exception being 35 or 40 microns) and the *cultivated type,* whose pollens measure from 35 to 50 microns, with the modal peak at 40 microns. According to Wodehouse, the tribe Hordeae, which includes the most important

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cereal grasses such as wheat, barley, and rye, has large pollen grains. Included in this tribe are also Lolium, Agropyron, and Elymus. The grains of all these, except of Lolium, range in size from 33 to 47 microns, while those of the latter are only 28 to 33 microns. *Zea mays*, with its pollen grains of 90 to 100 microns, has the largest pollen grains of the grasses, but since it is restricted to cultivation in North America, it plays no part in pollen analyses of bog sediments.

The exine of grass pollens is thin and without distinguishing markings, but always slightly rough. Wodehouse likens it to "the stippled surface of an ordinary stucco wall." This feature is best observed in empty grains. The intine is thin and hyaline, the interior is packed with starch grains, and has a small hyaline body diametrically opposite the pore.

The most characteristic feature of the grass pollens is the single germ pore. This consists of a thickened rim of the exine and a small aperture covered by a delicate transparent membrane in the middle of which is a conspicuous thickening, called the operculum. In the case of ovoidal pollen grains the germ pore tends to be located in the larger end. The pore is circular in shape, or nearly so, although the margin may be irregular. The rim stains quite deeply. The elastic membrane covering the aperture varies from 2.3 to 9.1 microns according to Wodehouse (8). The larger grains usually have the larger aperture. The operculum at the center stains quite deeply. Sears (7) says, "the distinct central operculum may be absent in fossil material."

The round, smooth pollen grains of the grasses are adapted for pollination by wind. Insect pollinated grains are usually sticky, and are characterized by spines and furrows which enable them to cling better to the bodies of the insects. Pollen grains of the same and closely related species tend to be alike, provided the environmental features are uniform. For instance, the exine of willow, which is chiefly insect pollinated, is thick and furrowed, while that of poplar, which is wind pollinated, is thin and lacking in furrows. The size is consistent with wind pollination. According to Wodehouse (8) neither very large nor very small pollen grains are ever wind pollinated. The grass pollens fall into the intermediate class. The largest pollen grains, like the pumpkin, with grains about 200 microns in diameter, and the four-o'clock, with grains 180 microns in diameter, are so large they cannot float easily ; and are insect pollinated. Small size seems to be a hindrance for pollen grains in leaving their anthers

or in separating from each other. Small floaters, like fungus spores, have a mechanism for throwing the spores clear of the plant and each other. Most plants lack this mechanism.

METHODS

The grasses included were selected from the following habitat groups :

I. AQUATIC. *Leersia oryzoides, Phragmites communis, Calamagrostis canadensis, Poa palustris, Glyceria septentrionalis, Zizania aquatica.*

II. WET LOWLAND. *Muhlenbergia racemosa, Phalaris arundinacea, Cinna latifolia, Spartina pectinata, Glyceria canadensis, Elymus villosus, Bromus kalmii, Elymus virginicus.*

III. MESOPHYTIC. *Triodia flava, Poa autumnalis, Festuca elatior, Dactylis glomerata, Poa sylvestris, Bromus purgans.*

IV. PRAIRIE. *Koeleria cristata, Sporobolus asper, Sporobolus heterolepis, Buchloe dactyloides, Bouteloua curtipendula, Andropogon scoparius, A. furcatus, Stipa spartea.*

Samples of pollen grains studied were collected from labeled specimens in the herbarium, and by means of forceps and a needle were placed on a clean slide. The grains were obtained from two or more plants collected at different localities. The grains were covered with a drop of warm gelatin colored with gentian violet, and the cover glass was affixed. Care was taken to clean the needle and forceps each time to prevent mixing of the species. The slides were allowed to stand until the shrunken grains had resumed the normal shape, and the dye had penetrated.

Measurements of 50 or more pollen grains were taken of each species studied. It was at times impossible to obtain enough pollen grains from the dried material to make counts of 100 ; in such cases results are based on a count of 50. Measurements were also made of the aperture wherever the pore was visible. Measurements were made under the high power of a binocular microscope with a magnification of 645X. Ellipsoidal or ovoidal grains were measured across the larger diameter.

Drawings of the 32 species are shown in figure 1. In the drawings the smallest, the largest, and the intermediate sizes are shown,
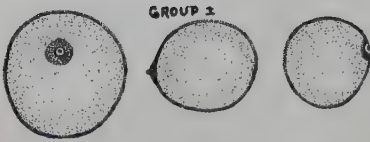
GROUP I

ZIZANIA AQUATICA
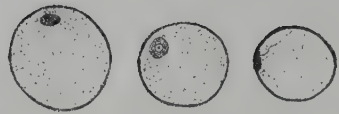
ELYMUS VILLOSUS

GLYCERIA SEPTENTRIONALIS

SPARTINA PECTINATA

POA PALUSTRIS

GLYCERIA CANADENSIS
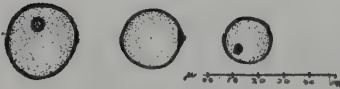
LEERSIA ORYZOIDES

CINNA LATIFOLIA

CALAMAGROSTIS CANADENSIS

PHALARIS ARUNDINACEA

PHRAGMITES COMMUNIS
GROUP II

MUHLENBERGIA RACEMOSA
GROUP III
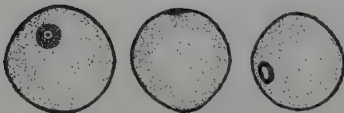
ELYMUS VIRGINICUS

BROMUS PURGANS
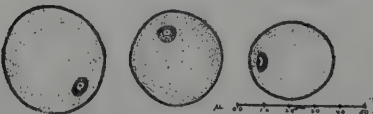
BROMUS KALMII

POA SYLVESTRIS

68
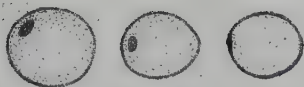
FESTUCA ELATIOR

STIPA SPARTEA

DACTYLIS GLOMERATA

ANDROPOGON FURCATUS

POA AUTUMNALIS
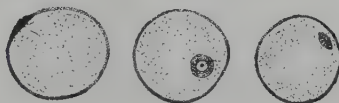
ANDROPOGON SCOPARIUS

TRIODIA FLAVA
GROUP IV
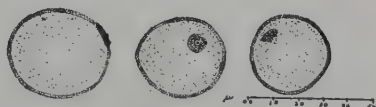
BOUTELOUA CURTIPENDULA
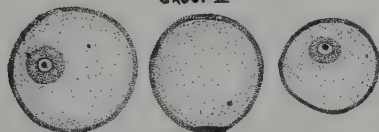
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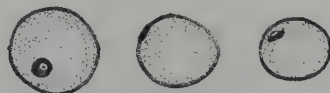
BUCHLOE DACTYLOIDES
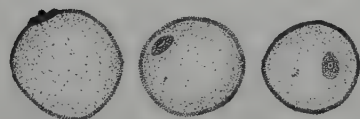
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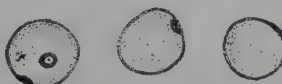
SPOROBOLUS HETEROLEPIS
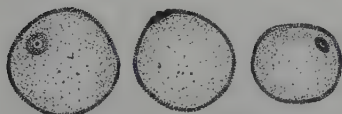
SORGHASTRUM NUTANS

SPOROBOLUS ASPER

PANICUM VIRGATUM

KOELERIA CRISTATA

GROUP III

Triodia flava

Poa autumnalis

Festuca elatior

GROUP I

Leersia oryzoides

Dactylis glomerata

Phragmites communis

Poa sylvestris

Calamagrostis canadensis

Bromus purgans

Poa palustris

GROUP IV

Glyceria septentrionalis

Koeleria cristata

Zizania aquatica

Sporobolus asper

Sporobolus heterolepis

GROUP II

Muhlenbergia racemosa

Buchloe dactyloides

Phalaris arundinacea

Bouteloua curtipendula

Cinna latifolia

Andropogon scoparius

Andropogon furcatus

Spartina pectinata

Stipa spartea

Glyceria canadensis

Panicum virgatum

Elymus villosus

Sorghastrum nutans

Bromus kalmii

Elymus canadensis

Elymus virginicus

Agropyron smithii

20 24 28 32 36 40 44 48   20 24 28 32 36 40 44 48

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RESULTS

In the aquatic species (group I) the size range was 19-50 microns. If *Zizania aquatica* were excluded, the range would be 19-35 microns. This species has a pollen size range of 38-50 microns. The walls of the grains appeared thinner than those of prairie grasses of similar size.

The smallest pollen grains studied fell into group I, but there was considerable overlapping with group II. The modal peak was 25 microns (12%). In the 8 species of the wet lowland (group II), pollen grains ranged in size from 25-46 microns, with modal peak (15%) at 31 microns. The mesophytic group (group III) consisted of six species whose size range was 24-39 microns, with the modal peak (14.6%) at 31 microns. The 12 prairie species of group IV ranged in size from 21-50 microns, with modal peak at 30 microns (11%).

DISCUSSION

It has already been stated that the identification of the grass pollens is a very difficult problem, even if only separation of genera is involved. Lewis and Cocke (6) state, "Only a pollen expert would dare even to guess at the specific or even the generic names of all the grass pollen found."

Cain (1) in his study of 12 species of Pinus found that no readily diagnostic morphological characters could be discovered on basis of which to separate them, and so he sought a differentiation on the basis of size-frequency. In this study Cain found that certain of the species appear to be distinguishable by means of the range, shape, and mode of their size-frequency curve. Then he made a set of size-frequency curves for the three pine species of fossil pollen he was trying to identify. By matching these curves of the three fossil unknowns with the known modern pollen he thinks that he was able to identify two of the unknown, and to narrow his choice down between two species for the third unknown.

Size variation is no doubt a very satisfactory basis on which to classify biological forms, provided there is not too much overlapping of the sizes compared. This would fog, or perhaps even frustrate, a satisfactory differentiation between two species, or groups of species. Such a method also becomes more difficult to apply with increasing number of species involved. Study of grasses entering into a pollen analysis of bog sediments must necessarily include a large number of

species in order to cover the source of pollens from which contributions were made to a lake or bog. Since grasses represent almost the whole range of ecological situations, from extreme hydrophytism to extreme xerophytism, it seemed essential that four common habitat types be represented in the analysis by four groups of the most common and the most abundant species found in such habitats, as described previously. No attempt was made to determine the possible variation in size of pollen grains of the same species in different geographical locations. Cain (2) has shown that a variation exists in size of pollen grains of the same species of pine in different parts of the United States, and so there may very likely be the same condition prevailing in pollens of grasses. However, this would not likely eliminate the prime consideration in this problem, i. e. the similarity of pollen from Zizania and those of the dominant prairie grasses.

Separation on basis of pollen size of aquatic and wet lowland grass groups from the prairie grass group would be possible to a fair degree because of larger size of pollens of the prairie group if it were not for the intrusion of *Zizania aquatica* into the size group. Shape of its pollen and shape and characteristic of the pore are so closely the same as those of the Andropogons and Sorghastrum that this one species practically nullifies all attempts at a separation of aquatic and prairie groups.

The problem is also intensified by the habit of Zizania to grow in such profusion when shallowing water offers suitable habitat that it could contribute the major part of grass pollen at a given foot-level of a bog. Results of the present study gave no clue to a solution of the problem. However, the results indicate that if the peaks fall into the lower range of grass pollens, i. e. 19-39 microns, prairie conditions can hardly be associated.

SUMMARY

1. The pollen grains of 32 species of grasses were studied.

2. The grasses considered were divided into four groups, representing aquatic, wet lowland, mesophytic and prairie habitats.

3. Drawings were made of each species studied, and a size frequency curve was constructed.

4. Most of the species seem to have a single distinct high peak in the size-frequency, which, unfortunately, was identical for different species.

5. The modal peak for group I was 25 microns. The size range was 19-50 microns.

6. *Zizania aquatica* was the only member of group I with pollen size greater than 35 microns, and so overlaps with the prairie group. It seems to have a thinner cell wall than pollens of the same size from prairie species.

7. The modal peak for both groups II and III centered at 31 microns. Size range for group II was 25-46 microns and for group III it was 24-39 microns.

8. Size range for group IV was 21-50 microns, with a modal peak at 39 microns.

9. As a whole, the pollens of prairie grasses are markedly larger than those of other ecological groups, but since *Zizania aquatica* has pollen similar to that of the Andropogans and Sorghastrum it is practically impossible to separate prairie from aquatic grasses on basis of pollen size difference.

ACKNOWLEDGMENTS

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PLANT SUCCESSION AT LONG POND, LONG ISLAND, NEW YORK*

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University of Notre Dame

Kettle hole lakes of glacial origin are of frequent occurrence on the north side of Long Island, New York. These lakes vary in size and depth. Long Pond is a kettle hole lake located about eight miles south of Wading River on Long Island. It is an irregularly shaped lake approximately one-half mile wide and one-half mile long at the present time (See fig. 1 for the shape of the lake and the location of the areas which were studied statistically.) There are several small ponds that are cut off now or are in the process of being cut off from the main body of the lake. The small ponds that are now cut off were a part of the lake in 1907 and 1908. Local residents say that the water level of the lake has fluctuated considerably in past years. During the different period of drought, the water level has been lowered and marked invasions of plants towards the center of the lake have occurred. With the return of higher water levels in years of plentiful rainfall many plants that had advanced toward the center of the lake have been drowned and this has resulted in a recession of the zones of vegetation. Evidence of this is found on the west side of the lake where two lobes of the lake are almost cut off. Many trees of *Pinus rigida*[1] nine and ten years of age, are found in areas that are now moist (fig. 2). These were established when the water level was lower and the area much drier. Since the rise of the water, several have died and the remainder now living in these present moist areas are of low vitality. The work of Graham and Henry (1933)[2] at Deep Pond, about two miles from Long Pond, substantiate the reports of fluctuating water level with the attendant plant invasions and recessions.

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[1] Nomenclature follows Gray's Manual 7th Ed. unless otherwise noted by the addition of name authorities.

[2] GRAHAM, H. W., AND L. K. HENRY. 1933. Plant succession at the borders of a kettlehole lake. Bull. Torrey Bot. Club. 60: 301-315.
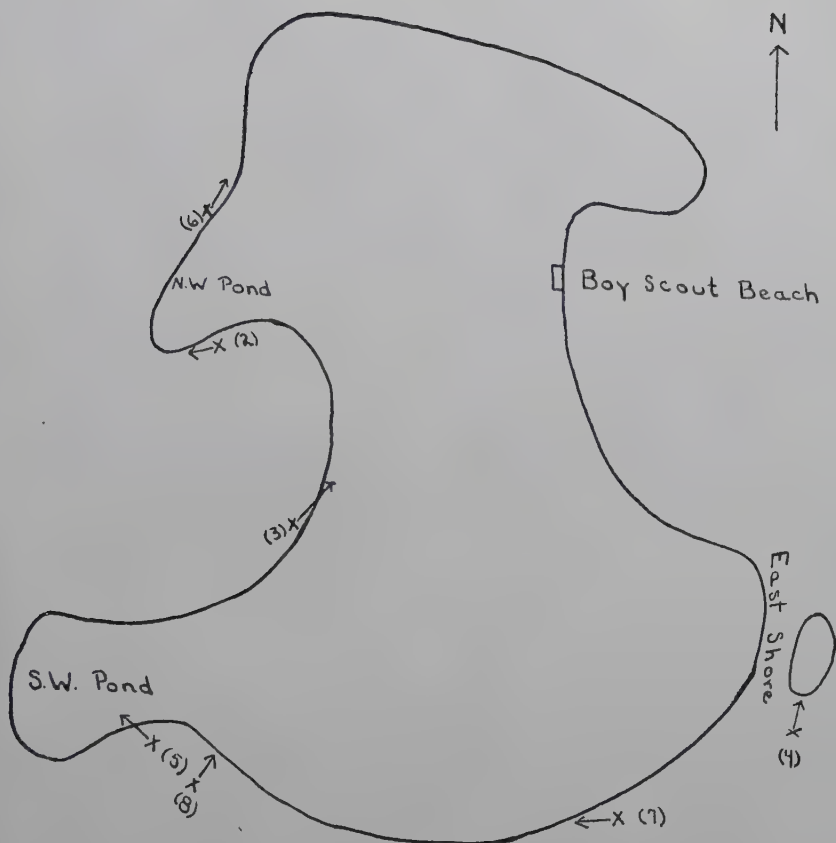
Fig. 1. Outline of Long Pond. The numbers refer to the following figures
used in this text. The X marks the position of the camera and the arrow the
direction of the exposure.

The composition and structure of the communities was determined
by the quadrat method. Coverage and frequency counts were made
and the dominants of each community were ascertained. From these
studies, together with field observations, the successional tendencies
were obtained and the following successional diagram made. A dis-
cussion of each community follows the successional chart.

Pinetum rigidae

Cephalanthetum occidentalis

Panicetum virgatis

Beach community

Mariscetum mariscoides

Eleocharetum Robinsii

Calamagrostidetum canadensis

Juncetum militaris

Castalietum odoratae

Submerged aquatics
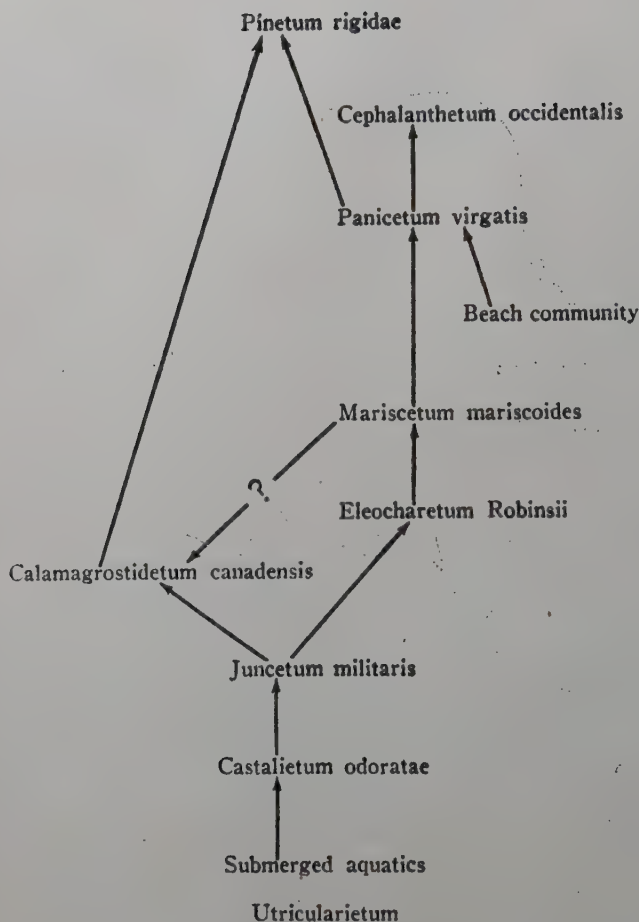
Utricularietum

Diagram of the succession of plant communities at Long Pond.

UTRICULARIETUM AND CASTALIETUM

Throughout the center of the lake and approaching the shores are found species of submerged plants which make up a community that will be called the Utricularietum because of the great abundance of *Utricularia purpurea* and *U. macrorhiza* L. C. Other species occurring there are *Vallisneria spiralis, Potamogeton Oakesianus, P. pectinatus* and *Myriophyllum humile* and algae (of which no species list was made). These species often form dense areas of vegetation. In more

Fig. 2. The border of the northwest pond showing young pines growing in an area that is now moist. The open strip found between the small pines on the right and the larger pines on the left is occupied by Drosera et al.

Fig. 3 Showing the nearly pure stand of Juncus militaris in the water from a depth of one to three feet.

shallow water, from two feet to a depth of about eight feet, water lilies are found. Their leaves cut off a considerable amount of light from the submerged plants. This results in shading out the Utricularietum and the establishment of the Castalietum. Large amounts of plant material are annually deposited by the species of the Utricularietum and the bulky species of the Castalietum. The latter community includes *Castalia odorata, Brasenia Schreberi, Potamogeton Oakesianus* and near the shore *Juncus militaris* becomes established in about three feet of water. The Castalietum extends shoreward to a depth of about two and one-half feet of water. The deposition of organic matter on the bottom of the lake is augmented by the inwash of sediment from the shore so that gradually the whole lake is being filled in, and suitable habitats for the Castalietum are being formed nearer the center of the lake.

JUNCETUM

Due to the gradual upbuilding of the lake, the Castalietum is advancing towards the center and is followed by the Juncetum, found in one to three feet of water. *Juncus militaris* forms nearly a pure stand (fig. 3). Mixed with it is an occasional individual of *Euthamia minor* (Michx.) Greene and *Coreopsis rosea*. These two species are remnants of the drier years and are now merely hanging on in this community. Young plants of these two species are found only on the beach.

Further successional units are best developed in the two small lobes of the lake which are being cut off at present and which are filling in very rapidly (figs. 4 and 5). Here, too, the aforementioned Utricularietum, Castalietum and Juncetum are found. An occasional mat of dead lily rhizomes covered with *Drosera rotundifolia, D. intermedia* Hayne, *D. filiformis* and *Dulichium arundinaceum* is found floating in the center of the ponds. During the drought years the water receded from this area and the lily rhizomes died. At that time they became filled with air and the encroaching shore vegetation grew over and around these dead rhizomes. When the rainfall later increased and the water returned to the pond, the dead rhizomes floated to the top of the water bearing with them the plants that had started to grow upon them (namely those species mentioned above). In some places either the Eleocharetum or the Calamagrostidetum replaces the Juncetum.

Fig. 4. This is a small pond on the east side of the lake which is now completely separated from the main body of water. The vegetation is rapidly filling in this pond.

Fig. 5. A view of the southwest lobe of the lake that is filled in.

ELEOCHARETUM

If the Eleocharetum develops, *Eleocharis Robbinsii, Eriocaulon articulatum, Sagittaria teres, Sparganium americanum* and *Dulichium arundinaceum* are found. This community is of very local importance and is found only in small areas. This is replaced either by the Calamagrostidetum or Mariscetum.

CALAMAGROSTIDETUM

The Calamagrostidetum is found from 4 to 20 inches above the water level, which is about the same habitat as the Panicetum. *Calamagrostis canadensis* is the dominant species having a frequency of 100% and a coverage of class 4.[3] Other members of this community

are:	Frequency	Coverage
Aster ericoides	76	x
Lycopus sessilifolius	68	x
Rhus copallina	64	x
Rubus frondosus	52	x
Rubus hispidus	40	x
Euthamia minor	36	x
Eupatorium hyssopifolium	28	x
Juncus acuminatus	16	x
Mariscus mariscoides (Muhl.) Kuntze	16	x
Spiraea tomentosa	12	x
Steironema lanceolatum	12	x
Viola lanceolata	8	x
Pinus rigida	8	x
Andropogon scoparius	4	x
Betula populifolia	4	x
Eupatorium perfoliatum*	4	x
Drosera intermedia	4	x
Solidago rugosa	4	x
Lobelia spicata	4	x

* More frequent outside of the quadrats.

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[a] Frequency was determined by the per cent of the total number of quadrats in which the species appeared (rooted). Coverage is the extent (surface and volume) covered or occupied by the individuals of each species and is expressed as follows:

> x—species covering less than 1% of the surface.
> 1—species covering 1— 5% of the surface.
> 2—species covering 6—25% of the surface.
> 3—species covering 26—50% of the surface.
> 4—species covering 51—75% of the surface.
> 5—species covering 76—100% of the surface.

(Cain, S. A. Certain phytosociological concepts. Ecol. Monog. 2: 475-508. 1932.)

Panicum virgatum and *Agalinis purpurea* (L.) Pennell were found but they were outside of the quadrats.

Several of the Pine Barrens species are occasionally found in this community. This is to be expected due to the proximity to the Pine Barrens vegetation. *Rhus copallina* is obviously an invader from the Pine Barrens and probably entered during drier times. Eventually the Calamagrostidetum is replaced by the Pinetum.

MARISCETUM

In some places the Mariscetum replaces the Eleocharetum. This community is characterized by the paucity of species. *Mariscus mariscoides* (Muhl.) Kuntze is the dominant species having a frequency of 100% and a coverage of class 4. The other species are:

	Frequency	Coverage
Lycopus sessilifolius	80	x
Calamagrostis canadensis	70	x
Euthamia minor	40	x
Eupatorium hyssopifolium	20	x
Spiraea tomentosa	20	x
Steironema lanceolatum	10	x

Panicum virgatum was found outside of the quadrats at the upper limits of this community. An occasional *Pinus rigida* was found here also.

Along the north edge of the northwest pond three dead pines were found at the edge of the Mariscetum showing that the Pine Barrens vegetation had invaded this area in previous drier times. Undoubtedly the shade cast by the stems of Mariscus is responsible for the death of many species in this community and accounts for the paucity of the flora here.

PANICETUM

The Panicetum succeeds the Mariscetum. It is a prominent community found all along the northwest and north shores of the lake (fig. 6). (The northeast shore has been greatly disturbed but apparently was formerly occupied by the Panicetum.) The Panicetum occupies the beach from the edge of the water back to the shrub zone on the west and north shores. The east and south side of the lake is bordered by a narrow strip of vegetation that has only an occasional clump of Panicum and a large number of other herbaceous species. The east beach is bare and sandy. The prevailing westerly wind has

Fig. 6. The tall and dense stand of Panicum virgatum that is prominent along the northwest and north shore of the lake.

Fig. 7. The beach vegetation of the east shore. Note the three zones of vegetation.

prevented the establishment of plants in this area. Even the hydrophytes in front of the beach are absent. However, a short distance to either side of the bare area, away from the direct influence of the wind, plants have become established on the beach and others in the water. Here, on the beach, appear three distinct zones of vegetation (fig. 7). These zones mark the advance of pioneer species into the bare area left by each recession of the lake. The zones vary in width. Measurements were taken along this portion of the lake in order to determine the width of those zones. The first zone, nearest the beach varied from 100 to 220 cm. in width, the second 80 to 160 cm. and the third 80 to 190 cm. These variations in width of the zones were due to several things: variations in the steepness of the slope of the beach, or to the shade cast by tall pines above the beach, or to an occasional alluvial fan. The zone nearest the lake has the fewest species. This is the area that was most recently laid bare and is the most moist zone. The third zone, and farthest away from the lake, has been out of water for the longest time and, as might be expected, has the largest number of species. Several species found in the surrounding Pine Barrens have been able to become established in the two upper zones.

Data from quadrat studies (table I) of the beach vegetation show that these three zones are not very distinct floristically, nor do they show organization, hence they do not merit the rank of a successional unit. For this reason the term beach community has been used.

In table I, zone 3, it will be noticed that a number of the nearby Pine Barrens plants are migrating into the beach community. In some places *Panicum virgatum* is becoming established in the upper zone along the south shore and indicates that a community comparable to the Panicetum of the west and north shores may eventually develop. In a few places a shrub community of Myrica and Cephalanthus replaces the beach community in advance of the Pinetum.

TABLE I

Species of Beach Community	Zone 1		Zone 2		Zone 3	
	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.
Cyperus dentatus ctenostachys	100	x	90	1	90	x
Coreopsis rosea	100	x	100	x	40	x
Gratiola aurea	70	x	80	x	60	x
Xyris caroliniana	50	x	90	x	60	x
Eriocaulon articulatum	50	x	30	x		
Viola lanceolata	20	x	70	x	60	x
Polytrichum commune	20	x	60	x	40	x

TABLE I—(Continued)

Species of Beach Community	Zone 1		Zone 2		Zone 3	
	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.
Juncus pelocarpus	20	x	30	x	10	x
Euthamia minor	10	x	40	x	70	x
Juncus acuminatus	10	x	30	x	30	x
Drosera intermedia	10	x	60	x	60	x
Bidens sp.?	10	x	50	x	30	x
Castalia odorata	10	x	30	x		
Agrostis alba	10	x	80	x	80	x
Myriophyllum humile	10	x	10	x		
Cyperus Nuttallii	10	x				
Hypericum canadense			90	x	70	x
Rhynchospora glomerata			70	x	60	x
Fuirena squarrosa			60	x		
Panicum oricola			50	x	100	1
Lycopus sessilifolius			90	x	50	x
Juncus dichotomus			40	x	40	x
Steironema lanceolatum			40	x	10	x
Fimbristylis autumnalis			30	x		
Drosera filiformis			30	x	60	x
Sphagnum sp.?			20	x	10	x
Rhexia virginica			20	x	40	x
Dulichium arundinaceum			10	x		
Philonotis fontana			10	x	10	x
Stachys hyssopifolia			10	x		
Andropogon scoparius			10	x	10	x
Polygonella articulata			10	x	20	x
Juncus Greenei			10	x	30	x
Panicum virgatum			10	x	20	x
Calamagrostis canadensis			10	x	10	x
Agalinis purpurea			10	x	10	x
Rubus hispidus			10	x	10	x
Eleocharis melanocarpa			10	x	10	x
Hypnum sp.?			10	x		
Deschampsia flexuosa					10	x
Aster dumosus					10	x
Myrica carolinensis					10	x
Betula populifolia					10	x
Pinus rigida					10	x
Gnaphalium obtusifolium L.					10	x
Melampyrum lineare					10	x
Eupatorium perfoliatum					10	x
Eupatorium hyssopifolium					10	x
Polygala polygama					10	x
Linaria canadensis					10	x

TABLE II

Species of the Panicetum	Frequency	Coverage
Panicum virgatum	100	4
Stachys hyssopifolia	60	x
Eupatorium hyssopifolium	60	x
Pallavicinia Lyelli	44	x
Euthamia minor	40	x
Aster dumosus	36	x
Lycopus sessilifolius	20	x
Rubus hispidus	20	x
Cyperus dentatus ctenostachys	20	x
Cephalanthus occidentalis	16	x
Hypericum canadense	12	x
Rubus frondosus	12	x
Rhus copallina	12	x
Gnaphalium obtusifolium	12	x
Myrica carolinensis	8	x
Aster sp.?	8	x
Juncus acuminatus	8	x
Viola lanceolata	8	x
Fuirena squarrosa	8	x
Calypogeia Trichomanis	8	x
Bidens sp.?	8	x
Fragaria vesca	8	x
Steironema ciliatum	8	x
Gratiola aurea	4	x
Melampyrum lineare	4	x
Solidago rugosa	4	x
Cassia nictitans	4	x
Eriocaulon articulatum	4	x
Xyris caroliniana	4	x
Panicum oricola	4	x
Polygonum scandens	4	x
Oldenlandia uniflora	4	x
Agalinis purpurea	4	x
Linaria canadensis	4	x
Cuscuta Polygonorum	4	x
Coreopsis rosea	4	x
Pinus rigida	4	x
Achillea Millefolium	4	x
Desmodium marilandicum	4	x
Lespedeza repens	4	x
Eupatorium perfoliatum	4	x

Oenothera biennis, Lactuca canadensis, Chrysopsis mariana, Lechea villosa, and *Rubus villosus* were found outside of the quadrats.

As is indicated by the frenquency and coverage figures in table II, *Panicum virgatum* is by far the most important species with only

Stachys hyssopifolia and *Eupatorium hyssopifolium* appearing in any appreciable quantity. The flowering stalks of the Panicum are about six feet high. These shade out many of the other species. The shading effect is shown in the longer, more slender internodes, narrower leaves and the more succulent growth of many of these species. *Cephalanthus occidentalis, Myrica carolinensis, Vaccinium vacillans, Rhus copallina* and *Pinus rigida* have become established at the upper edge of the Panicetum. Where these woody species have become established the Panicum is dwarfed. This evidence shows that the Panicetum will eventually be invaded by the shrub community and finally the Pine Barrens flora.

Fig. 8. A general view of the lake showing the Pine Barrens surrounding it.

PINETUM

The Pinetum is the dominant vegetation in this region of Long Island, is found all around Long Pond and is at present gradually encroaching upon the border of the lake (fig. 8). *Pinus rigida* is the dominant species of this community and *Quercus alba, Q. coccinea,* and *Q. stellata* are important associates. *Populus tremuloides, P. grandidentata, Nyssa sylvatica* are the other tree species of the Pinetum. In the undershrubbery *Quercus ilicifolia* is the dominant species

and its important associates are *Neopieris mariana, Gaylussacia baccata, Rhus copallina,* and *Myrica carolinensis,* while *Xolisma ligustrina, Vaccinium vacillans, Smilax rotundifolia, Eubotrys racemosa* and *Aronia melanocarpa* are found in less abundance. The characteristic herbs are *Solidago odora, Melampyrum lineare, Eupatorium hyssopifolium, Chrysopsis falcata, Chrysopsis mariana, Carex pennsylvanicum, Deschampsia flexuosa,* and *Polygonella articulata.* Other herbs are *Solidago nemoralis, Euthamia minor, Andropogon scoparius, Panicum virgatum* and *Aster ericoides.*

GEOGRAPHIC DISTRIBUTION OF THE SPECIES

The late summer flora of Long Pond is made up of groups of species having unlike ranges of distribution. As would be expected, the group having the largest number of species is that which has a widespread distribution. This group can be subdivided into two divisions, (*a*) species that are widespread throughout the area east of the Mississippi River and eastern Canada; (*b*) a smaller group of species that are found on the continent of North America and other places (Europe, Asia or West Indies, etc.). The following species have the distribution of group (*a*):

Andropogon scoparius, Aster dumosus, A. ericoides, Calamagrostis canadensis, Cassia nictitans, Castalia odorata, Cephalanthus occidentalis, Desmodium marilandicum, Drosera rotundifolia, Dulichium arundinaceum, Eleocharis Robbinsii, Eupatorium perfoliatum, Fragaria vesca, Fuirena squarrosa, Gnaphalium obtusifolium, Gratiola aurea, Hypericum canadense, Lactuca canadensis, Lechea villosa, Linaria canadensis, Lobelia spicata, Juncus acuminatus, Mariscus mariscoides, Myrica carolinensis, Oenothera biennis, Panicum virgatum, Polygala polygama, Polygonum scandens, Rhexia virginica, Rhus copallina, Rynchospora glomerata, Solidago rugosa, Sparganium americanum, Steironema ciliatum, Steironema lanceolatum, Utricularia macrorhiza, Utricularia purpurea, Vaccinium vacillans, Viola lanceolata, Xyris caroliniana.

The following belong to group (*b*) of the widespread species:
Achillea Millefolium, Agrostis alba, Brasenia Schreberi, Drosera intermedia, Potamogeton pectinatus, Vallisneria spiralis, Deschampsia flexuosa, Eriocaulon articulatum. These widespread species are not confined to any particular successional unit but are found in all of the communities at Long Pond.

A large number of Coastal Plain species are found at Long Pond.

This is to be expected because the southern part of Long Island is at the northern limit of the present Atlantic Coastal Plain. Although the Long Pond region was glaciated it is only a short distance from the Coastal Plain Province and those species have had ample time and opportunity to migrate into this area. These Coastal Plain species may be divided into two groups. Group (*a*) is made up of species that are found on the Atlantic Coastal Plain and in the Great Lakes region. Group (*b*) is made up of species that are found along the Atlantic coast and in adjacent provinces. The following comprise group (*a*): *Coreopsis rosea, Cyperus Nuttallii, Eleocharis melanocarpa, Euthamia minor, Lycopus sessilifolius, Oldenlandia uniflora, Polygonella articulata, Sagittaria teres.* These make up group (*b*): *Agalinis purpurea, Chrysopsis mariana, Cuscuta Polygonorum, Eupatorium hyssopifolium, Fimbristylis autumnalis, Juncus dichotomus, Melampyrum lineare, Pinus rigida, Rubus frondosus, R. hispidus, Spiraea tomentosa, Stachys hyssopifolia.*

The third group of species may likewise be divided into two subdivisions. In group (*a*) are species of a local distribution on the northern portion of the present Coastal Plain. In group (*b*) are species that are limited in the eastern part of the United States. Group (*a*): *Cyperus dentatus ctenostachys, Drosera filiformis, Panicum oricola, Potamogeton Oakesianus, Rubus villosus..* In group (*b*) are *Betula populifolia, Juncus Greenei, J. militaris, J. pelocarpus, Myriophyllum humile.*

In the late aestival flora there are, then, the following groups of species: those that are widespread; those that are found mainly on the Coastal Plain; species that have a limited distribution in the eastern portion of the United States; and a few species that are found in a limited area on the northern end of the Coastal Plain. A northern element in this Long Pond flora is conspicuous by its absence.

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The Herbarium
University of Notre Dame
Notre Dame, Indiana

THE PLANT ASSOCIATIONS OF THE CARSON DESERT REGION, WESTERN NEVADA*

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Except for scattered references of a generalized nature, little is recorded concerning the structure of vegetation in the arid and semi-arid portions of the western Great Basin. The delineation of the associations[1] of a part of this area and their particular environments is the prime funtion of this paper.

The name "Carson Desert" has long been applied to the region surrounding the Carson Sink and the lower Carson River in western Nevada. For the purposes of this investigation, the term "Carson Desert Region" will include not only the Carson Desert but also the deserts surrounding the lower reaches of the Truckee River, Pyramid Lake, the Walker River, and Walker Lake. The resulting area is elongated in a northwest-southeast direction with its central axis parallel to and about 75 miles northeast of the summit ridge of the Sierra Nevada. About 5,000 square miles of territory are involved. The dry slopes and benches of the region are mainly used as winter range for livestock although, in most places, the grazing is very light or even absent. Agricultural land, irrigated and reclaimed, occupies a substantial acreage on the deep soils of the valley floors, particularly in the Fallon region south of Carson Sink.

GEOLOGY

The region is entirely within the Great Basin and, therefore, one of interior drainage. The topography is fairly typical of the Basin-and-Range Province with fault block mountain ranges more or less paralleling the meridians and separated by rift valleys or grabens. The floors of the valleys lie at elevations approximating 4,000 feet

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[1] The association as used here is that of the Zurich-Montpellier school as recommended by the Sixth International Botanical Congress, 1935. The association is considered to be made up of one or more unions. (See Lippmaa, 1939.)

above sea-level while the crests of the ranges average about 8,000 feet in elevation. By far the greater part of the Carson Desert region lies below 5,000 feet and, in this article, only that vegetation lying below 6,000 feet will be considered.

Most of the region was covered during the pluvial and glacial periods of the Pleistocene by the southern part of Lake Lahontan. Russell (1885) gives 4,378 feet above sea-level as the average elevation of the highest shoreline of this lake. Lake-laid sediments now cover almost all of the Carson Desert region below this elevation. They consist primarily of interbedded gravels, clays, and sands whose depth ranges from a few inches near the upper limits of the lake to well over a hundred feet in many places. Two types of post-Lahontan accumulations overlie the old lake sediments in a number of places. The first of these consists of aeolian sands of a light color and, therefore, clearly of extraneous origin in this region of dark volcanic rocks. Many of these dunes are active but the great majority are flat and quiescent and covered with a distinctive vegetation. Mud flats or playas constitute the second kind of post-Lahontan sediment. The lower parts of those rift basins not occupied at present by permanent lakes are filled during winters and wet years with shallow temporary lakes. Silts, clays, and salts carried into these playa-lakes are left behind upon the evaporation of the water during the summer months. Because of salinity and periodic drowning, most of the playas are completely devoid of vegetation except around the edges. They are known locally as "alkali flats."

The mountains and hills consist principally of basalts, andesites, and other basic lavas. They are covered by a thin, often broken, mantle of residual gray desert soils. Extending from the lower slopes are numerous alluvial fans and bajadas.

CLIMATE

Lying in the rain-shadow of the Sierra Nevada, the climate of the valley floors and the lower hills is distinctly arid. The higher slopes are semi-arid. Only in scattered places at the highest elevations does the climate approach humid types in the ranges immediately contiguous to the desert. Thornthwaite (1941) reports precipitation-effectiveness indices of below 16 for most of the Carson Desert region. According to his maps, this desert area lies in a narrow arm of aridity extending up the eastern side of the Sierra Nevada from the more

extensive arid regions of southern Nevada, southeastern California, and western Arizona.

The mean annual precipitation at the following stations is probably typical of the greater part of the area: Fallon, 4.98 inches; Fernley, 5.29 inches; Lahontan, 4.54 inches; and Schurz, 5.68 inches. The precipitation shows a distinct winter maximum such as might be expected in a region lying fairly close to a west coast in the middle latitudes.

The climate is neither excessively hot in summer nor extremely cold in winter. Fallon shows an average January temperature of 29.8° F. while the July average is 73.1° F. . At Yerington, the averages for the same months respectively are 30.3° F. and 70.5° F. . Because of the aridity and altitude, there is a broad range between night minima and day maxima.

LITERATURE

The first botanical observations in the Carson Desert region were made by Frémont (1845) during January, 1844. He describes sagebrush vegetation, the cottonwoods along the rivers, and the greasewood on the alkali flats. He failed to note, however, the several distinct types of true desert vegetation through which he passed in crossing from the Truckee to the Carson River over the fairly level country of what is now known as Swingle Bench. He merely mentions this stretch as being covered "with small sage bushes."

Of the publications of the several taxonomists who collected in the region during the latter part of the nineteenth century, the report of Sereno Watson (1871) of his botanical explorations during 1868 contains the best vegetational descriptions. His generalized descriptions are quite accurate. Watson did not, however, clearly distinguish the communities lying in the true desert between the sagebrush on the higher elevations and the greasewood of the playas.

In more modern times, the vegetational types of the Bonneville Basin in Utah have been delineated by Kearney and his co-workers (1914) and by Flowers (1934). The communities which they describe as occurring on the more saline soils are quite like those on similar soils in the Carson Desert region. However, the upland desert communities, both successional and climax, which cover the greater part of the Carson Desert are distinctly different from those in the Bonneville region. A number of papers have been written on the vegetation of the warmer deserts in Arizona and southeastern

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California. Notable among these are the works of MacDougal (1908), Shantz and Piemeisel (1924), Parish (1930), Shreve (1936, 1942), and Nichol (1937). In some respects, a close relationship seems to exist between the vegetation of the southern deserts and the upland communities of the Carson Desert.

Clements (1920) considers all of the shrubby vegetation of the drier parts of the Great Basin as belonging to what he calls the Atriplex-Artemisia association. Under this, he has established a great number of consociations based upon the apparent dominance of one shrubby species here and another there. The result is an extremely heterogeneous grouping of communities into a large and vague category whose structural bonds are open to question. The existence of numerous areas where a single species holds complete dominance can certainly be substantiated. However, most areas are populated by communities characterized by two or more co-dominants. In addition, the almost total lack of quantitative data fails to measure the degree of dominance or to bring out the true relationships between the consociations

Shantz (1924, 1925) has, perhaps, the most adequate descriptions to date of desert vegetation in the western Great Basin. He divides the vegetation in this region into two main types: sagebrush (northern desert scrub) and greasewood (salt desert scrub). Each of these he subdivides into three main associations under which are grouped a number of minor communities somewhat analagous to the consociations of Clements. Although descriptive only, the physiographic and edaphic array of the communities, as included, is rather clearly portrayed.

METHODS

Numerous reconnaissance trips were made into the Carson Desert region during 1939 and 1940 in order to become familiar with the vegetation and to set up an objective delineation of the communities. Fifteen distinct associations were established. Four of these, the little greasewood-shadscale type, the dalea type, the big greasewood type, and the big greasewood-shadscale type constitute by far the greater part of the natural vegetation of the region. These particular associations, therefore, were selected for quantitative study.

In 1941, ten stations were chosen for analysis in the little greasewood-shadscale association, ten in the Daleetum, three in the big greasewood association, and two in the big greasewood-shadscale

type. The stations were well scattered throughout the region. Presence lists of all shrubby and herbaceous species[2] at each station were compiled for both 1941 and 1942. The shrubby stratum was analyzed by quadrats at five stations in the little greasewood-shadscale type, at seven stations in the Daleetum, and at all stations in the big greasewood and big greasewood-shadscale associations. In the cases of the first two associations, 25 quadrats of 9 square meters each were laid out in the form of a latin square at each station with the exception of three stations in the dalea community where quadrats of 4 square meters each were used. In all cases, the interval between quadrats was 20 meters. The number and size of quadrats used in sampling the latter two communities varied from 25 quadrats of 4 square meters each to 10 quadrats of 100 square meters each, depending on the density of the stand. The herbaceous vegetation at all stations in the little greasewood-shadscale and dalea associations was sampled by 25 random throws of a 1/5 meter hoop at each station during the growing season of 1941. The data from the shrubby quadrats were analyzed for frequency, density (number of individuals per square meter), percentage of coverage of total area, and percentage of total shrubby cover. Density per square meter and frequency were determined for the herbaceous species from the data of the 1/5 meter quadrats. Since the densities of desert herbaceous species react sharply to differences in precipitation from year to year, it is realized that such data for just one year provide a mere starting point for quantitative work. The presence lists, however, developed over a longer period, provide a trustworthy record of the floristic composition of the herbaceous unions.

Soil trenches were dug in several stations of each of the four major associations and in several of the other types. Notes were made of the profiles and samples taken at certain depths. The samples from certain representative profiles were analyzed mechanically by a modification of the Buoyoucos (1928) method. Colorimetric indicators were used to determine soil pH.

The relative amounts of soluble salts in the soils of the several associations is expressed as K x 10[5] of a soil solution determined by conductance by the following method. The exact air-dry equivalent

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[2] The nomenclature is an attempt at the latest available synonymy. Authorities are given for all species in presence tables. For those not so listed, authorities are given at the first mention of the name in the text.

of 50 grams of oven-dry soil is weighed out and mixed with 250 ml. of distilled water in a tightly stoppered flask. The mixture is shaken periodically for 5 days and then filtered through a Pasteur-Chamberlain filter. The conductance of the filtrate is determined with a conductivity bridge equipped with a cathode ray tube null indicator. A dip cell with a constant of about 1.0 should be used and the filtrate brought to a constant temperature of about $20°$ C. in a water bath. The conductance of the filtrate is expressed as $K \times 10^5$ where $K = \frac{\text{cell constant}}{\text{resistance}}$. If the value $K \times 10^5$ is multiplied by a suitable factor, the parts per million of soluble material in the filtrate may be approximated and thence the percentage of such material in the soil. Further experimental work, however, is needed on such a factor before such absolute results are trustworthy.

ASSOCIATIONS

1. LITTLE GREASEWOOD-SHADSCALE ASSOCIATION
(*Sarcobatetum Baileyi*)

This association covers more territory within the Carson Desert region than any other community. It is clearly the matrix of the vegetation in this arid portion of the Great Basin where the precipitation is too low for the development of the sagebrush association. The floristic structure of the little greasewood-shadscale association is brought out in tables I, II, and III. Soil characteristics at three selected locations in the type are listed in table IX. Figure 1 presents the typical appearance of the community.

The little greasewood-shadscale association consists of three unions. The frutescent union is designated the *Sarcobatus Baileyi-Atriplex confertifolia* union. The Oryzopsis-Sphaeralcea union is perennial herbaceous and the Cryptantha-Coldenia-Gilia union is annual.

The characteristic species of the dominant union are *Sarcobatus Baileyi, Atriplex confertifolia,* and *Artemisia spinescens.* All are low, spiny, microphyll shrubs. These make up the bulk of the shrubby stratum. *Eurotia lanata* and *Lycium Cooperi* are often present but of low density and coverage. The perennial herbaceous union is typified by *Oryzopsis hymenoides, Sphaeralcea ambigua* subsp. *monticola,* and *Hermidium alipes.* At some stations, this union is fragmentary or even absent. It is seldom well developed in this particular association. The annual union is also poorly developed here. Of

Figure 1. Little Greasewood-Shadscale association on Lahontan sediments at Station 3, 15½ miles south of Fallon, Nevada. Principal dominants are *Sarcobatus Baileyi, Atriplex confertifolia*, and *Artemisia spinescens*. Note the erosion pavement and almost total absence of herbs.

the principal species, *Cryptantha circumscissa, Coldenia Nuttallii*, and *Gilia leptomeria*, only the first is common in the Sarcobatetum Baileyi. *Eriogonum vimineum* and *Glyptopleura marginata* are often present in this association but are of lesser importance than certain other species in the union as a whole. The growth of the herbs, especially that of the annuals, is restricted to the late spring months when the soil still retains the moisture added by the winter precipitation.

The little greasewood-shadscale association occupies well-drained soils developed from the Lahontan sediments and also the residual volcanic soils of the hills, especially those in the drier southern part of the region. The soils are usually sandy loams or silt loams with marked amounts of gravel scattered through the profile. The surface of the soil is always more or less covered with a desert erosional pavement of gravel or rock left as the result of wind erosion. In places, this pavement may be poorly developed, but often it almost

completely covers the soil. The soils of this type developed from Lahontan sediments are distinctly alkaline in reaction, approaching pH 9 in most cases. The residual soils of the hills are somewhat less alkaline. The upper 5 or 6 decimeters of the Lahontan sediment soils are low in soluble salts but there seem to be mild accumulations below this depth. The residual soils occupied by this association are shallow and relatively free of salts.

Over most of its area, this association presents an aspect of monotonous regularity characterized by rather evenly spaced, low, spiny shrubs separated from each other by barren soil covered with the rocks of its erosion pavement. At the five stations quantitatively analyzed, the total shrubby coverage ranged from only 5 to 12 per cent of the ground. In contrast to the even distribution of individuals over most of its area, there is a pronounced tendency, in some places on residual soils in the southern part of the region, for the shrubs of this association to become aggregated along small erosion channels. The prominent ribbons of shrubs are separated by miniature divides 10 to 15 feet wide and covered with an almost continuous erosion pavement.

The little greasewood-shadscale association is closely related to the shadscale community described by Shantz (1924). The principal difference seems to be that the association as described here is dominated by little greasewood (*Sarcobatus Baileyi*), a species which Shantz does not mention as a member of the community. At every one of the five stations where quadrat data were gathered, *Sarcobatus Baileyi* is clearly dominant, constituting over 50 per cent of the total shrubby cover in each case. The percentages of total shrubby cover shown by *Atriplex confertifolia* are in most cases close to 20 per cent.

This association appears to be the climatic climax of the region. Wherever the annual precipitation in this microthermal region falls below about 7 inches and there is no other source of water, the sagebrush association gives way to the little greasewood-shadscale association on normal mature soils. The shadscale association of Shantz is undoubtedly the counterpart of the Sarcobatetum Baileyi in similar regions to the east and north of the range of *Sarcobatus Baileyi*.

2. WINTER-FAT ASSOCIATION
(*Eurotietum lanatae*)

In several places in the northern part of the Carson Desert region, especially north and east of Pyramid Lake, there are pure stands of

winter-fat, *Eurotia lanata*. The environment of this association is similar to that of the little greasewood-shadscale type. Shantz (1925) states that Eurotia often becomes dominant where shadscale has been killed. It may be successional to the Sarcobatetum Baileyi or it may represent certain edaphic conditions slightly different from those characterizing that association. The winter-fat association probably provides the best winter range in the region but is far less abundant than the little greasewood-shadscale association.

3. DALEA ASSOCIATION
(*Daleetum polyadeniae*)

The dalea association is one of the most interesting communities in the region. It is limited to areas of stabilized dune sands which are rather extensive, particularly in the region between the bend of the Truckee River at Wadsworth and Leeteville on the Carson River. The Daleetum is also abundant on the dunes in the valleys of the

Figure 2. Dalea association on aeolian sand at Station 1, just west of Leeteville, Nevada. *Dalea polyadenia*, *Atriplex canescens*, and *Tetradymia comosa* are prominent.

eastern part of the Desert Mountains from the hills north of Schurz to Sand Springs at the east end of Eight-mile Flat. The floristic composition of this association is exhibited in tables IV, V, and VI. Table IX lists the soil characteristics at three typical stations. Figure 2 shows the general appearance of the Daleetum. .

The dalea association could be considered as a twin association (Katz, 1929) to the Sarcobatetum Baileyi, since the same herbaceous unions are present in both. The frutescent stratum in the Daleetum is occupied by the *Dalea polyadenia-Atriplex canescens* union. The characteristic species of this union are *Dalea polyadenia, Atriplex canescens, Tetradymia comosa,* and *Tetradymia glabrata.* All of these are intricately branched, non-spiny, microphyll shrubs of medium height. *Sarcobatus Baileyi* and other shrubby species of the little greasewood-shadscale association are often present as survivors of a sand-drowned Sarcobatetum Baileyi. The two herbaceous unions are very well developed in the Daleetum. This is especially true of the annual union which exhibits here a relatively high density of individuals and also a certain floristic richness, 39 species being present in the 10 stations intensively studied. In addition to *Cryptantha circumscissa, Coldenia Nuttallii,* and *Gilia leptomeria* from which the name of the union is derived, other characteristic species are : *Abronia turbinata, Euphorbia ocellata* var. *arenicola, Cryptantha micrantha, Oenothera deltoides* var. *Piperi, Phacelia bicolor,* and *Eriogonum pusillum.* The Oryzopsis-Sphaeralcea perennial union is conspicuous here but is not much different floristically from its composition in the little greasewood-shadscale association. One difference is the frequent presence of *Pentstemon acuminatus* in the dalea type. *Hermidium alipes* seems to be more rare in the Daleetum than in the Sarcobatetum. The annual vegetation is conspicuous in late spring when the upper few decimeters of the sandy soil are moist from the winter precipitation. This moisture is completely utilized by the middle of June when the annuals are in fruit.

The soil of the Daleetum is a light-colored, siliceous, aeolian sand ranging in depth from 5 to over 20 feet. The pH is only slightly alkaline, the range usually being from about pH 7 to pH 8. The percentages of soluble salts are lower than in any of the other soils of the region. The whole profile is remarkably uniform, consisting almost entirely of pure sand.

Most of these dunes are broad, flat, and stable and at first glance do not appear to be dunes. Some of them are several square miles

in extent. The dune sands cover the Lahontan sediments of gravels and clays and are, therefore, superimposed upon the substratum that normally supports the little greasewood-shadscale association. There are numerous places where this occupation has taken place rather recently. In these places, *Sarcobatus Baileyi* and *Lycium Cooperi* have acted as dune-formers. As the sand builds up, these two species are able to keep pace for some time and are, consequently, likely to remain as relicts in the Daleetum. The first shrub of the dalea association to invade is *Dalea polyadenia* itself. As the sand grows deeper other shrubby species appear. *Tetradymia comosa* seems to require the deepest sand of all, not appearing until the depth reaches 10 to 20 feet. Blowouts do occur, resulting in a resumption of active sand movement. Some of the dunes have extended out into the playas, bringing the dalea association into contact with the big greasewood association. In some places, also, the sand has been carried far up the mountains on the eastern sides of the valleys so that the Daleetum under such conditions occurs some distance above the highest Lahontan shore-line.

The ground cover of the shrubby stratum is somewhat greater in the Daleetum than in the little greasewood-shadscale type, ranging from 8 to 28 per cent at the seven stations where quadrat data were gathered. *Dalea polyadenia* is dominant but not predominant, making up on the average about 30 to 35 per cent of the shrubby cover. At all locations, *Atriplex canescens* showed lesser coverage than the Dalea in the same stand. *Tetradymia comosa* occasionally shares dominance with Dalea in the deeper sands.

The sandy soil and the relatively dense herbaceous vegetation of this association provide the environment for an abundant rodent population. Evidences of rodent activity are certainly less in the little greasewood-shadscale association even when immediately adjoining the Daleetum. Hall (1941) has found, that in almost all cases, the pallid kangaroo mouse (*Microdipodops pallidus*) is restricted to fine sands occupied by *Dalea polyadenia, Atriplex canescens,* and their associates. On the other hand, the dark kangaroo mouse (*M. megacephalus*) seems almost confined to the coarser soils containing gravel usually occupied by a different type of shrubby community.

The dalea association seems to exhibit relationship with certain of the associations of the warmer deserts of Arizona and southeastern California. One of the dominants, *Atriplex canescens,* is common on the sandy soils of the Southwest. Many of the herbaceous species

also range to the southern deserts. Floristically, this community could have evolved from Mohavian sources with the disappearance of Lake Lahontan.

4. Big greasewood association
(*Sarcobatetum vermiculati*)

The big greasewood association is the most extensive of the truly halophytic communities within the region. It occupies the saline clay soils around the margins of the playas where the subsoil is always moist and only the surface crust dries in late summer. The structure of the shrubby stratum at three stations is shown in table VII while the soil characteristics at two of these locations are listed in table IX. Figure 3 presents the typical field appearance.

Figure 3. Big Greasewood association on wet saline clay at edge of Hot Springs playa. Station 3, 8½ miles northeast of Fernley, Nevada.

The big greasewood association is very poor in species. The dominant union is the *Sarcobatus vermiculatus* union which consists of only two species: *Sarcobatus vermiculatus* and *Atriplex lentiformis* subsp. *Torreyi*. In many cases, the latter species is absent and only

big greasewood is present in pure stand. The sparse herbaceous flora usually consists of scattered clumps of seepweed, mainly *Dondia nigra,* and poorly developed patches of desert saltgrass, *Distichlis stricta* (Torr.) Rydb. Exotic chenopodiaceous herbs, notably *Salsola kali* var. *tenuifolia* and *Echinopsilon hyssopifolius* (Pall.) Moq. (*Bassia hyssopifolia* Kuntze), often invade this community after disturbance. At Station 1 in this type, patches of moss were present around the bases of the greasewood, being especially well developed where the greasewood had died.

The soil of this association is made up primarily of the finer fractions and varies in most cases from silt loams to clays. The surface soils are usually loamy and friable when dry, while the subsoils starting at a depth of about 3 decimeters tend to be heavy, prismatically jointed clay. In places, this situation may be reversed, the surface soil being a clay and the subsoil loamy. This raises the question as to whether the soils of the big greasewood association and the adjoining bare playas show true horizons or merely geological strata. Certainly, new material is constantly being washed or blown into the playas from the surrounding hills and ancient lake sediments. The soils seem to be solontchak with rather high alkalinity throughout the profile, ranging from pH 8.5 to about pH 9.5. The soils contain rather high quantities of soluble salts, the percentage increasing from the lower part of the profile to the upper. This is the result of evaporation of the soil water at the top of the profile which usually produces a whitish crust of salts over the soil surface by late summer.

The ground coverage of the shrubs in the big greasewood type is quite variable, depending evidently upon the salinity and alkalinity of the soil. The coverage varied from about 4 per cent to 24 per cent at the stations studied. *Atriplex lentiformis* subsp. *Torreyi* is more intolerant of increasing salt content of the soil than is the greasewood. The saltbush is completely absent from stands where the soil salinity is too high and drops out before greasewood as one approaches a barren playa through this association. Lowrance (1939) at Station 2 found myrmicine ants, possibly Pogonomyrmex, burying seeds of the Atriplex under the friable surface crust at a depth of from 5 to 10 centimeters. Since the soil at this depth is more moist and less saline than the surface soil, the establishment of this species of Atriplex in the presence of a salt crust may be dependent to some extent upon the ant.

In an attempt to find the limit of tolerance of *Sarcobatus vermicu-*

latus to salinity and alkalinity, samples were taken from the bare playa of Eight-mile Flat about 40 meters beyond the edge of a stand of big greasewood. The pH of this soil was 9.6 throughout the profile. The salinity of the surface soil was over 5 times that of the surface crust within a normal stand of the big greasewood type, while the subsoil contained over twice as much salt as is usually the case in the subsoil of a normal stand.

The rising and falling of the playa-lakes over the years has a profound effect on this association. There are places in the Hot Springs Flat, northeast of Fernley, now covered with water, which once supported a big greasewood community. This is evidenced by the numerous dead greasewood bushes far out in the shallow lake. Conversely, in a greasewood stand about 14 miles south of Fallon, there are numerous remains of Typha rhizomes still embedded in the soil. This latter case is probably due to the draining of the surrounding land for agricultural purposes.

5. Big greasewood-shadscale association
(*Atriplico-Sarcobatetum*)

This luxuriant association results from the simultaneous occurence of the *Sarcobatus vermiculatus* union with the *Sarcobatus Baileyi-Atriplex confertifolia* union. The composition of the two shrubby layers as analyzed at two stations is presented in table VIII. Soil characteristics at Station 1 are listed in table IX.

The big greasewood-shadscale association occurs between the playa communities and the upland associations where soil conditions are just right for its development. The community is particularly well developed around the smaller, drier playas of the higher elevations. It is not too common. It may be that some stands of this type have been destroyed in the establishment of agricultural land in the Fallon area. Both stands utilized in the present study are in the far northwestern corner of the region. Although many more analyses are necessary, the soil seems to be a solonetz with the upper 2 or 3 decimeters loamy, low in salts, and with the pH slightly above 7. At about 3 decimeters, there is a sudden transition to a heavy, alkaline (pH 9) clay with a slightly higher salt content. This zonation could be caused by the washing out of the salts in the upper part of the soil by an unusual height of the playa-lake at some time in the past. On the other hand, the upper layer of soil could represent outwash material from the hills such as might be deposited in a bajada. This

geological explanation for solonetz has been proposed by Schert (1935) in Hungary as cited by Jenny (1941).

In each of the two stands studied, the total shrubby cover was almost exactly 30 per cent of the area of the stand. The union represented by *Sarcobatus vermiculatus* and *Atriplex lentiformis* subsp. *Torreyi* is clearly dominant, making up from 70 to 80 per cent of the total shrubby cover. The low shrub stratum is occupied principally by *Atriplex confertifolia* and *Artemisia spinescens* of the *Sarcobatus Baileyi-Atriplex confertifolia* union. *Sarcobatus Baileyi* is rare or absent in this association. *Tetradymia spinosa, Grayia spinosa, Eurotia lanata,* and *Kochia americana* S. Wats. and its variety *vestita* S. Wats. are also present. No intensive survey was made of the herbaceous vegetation of this association. *Dondia nigra* seems to occur in the wetter spots, while most of the herbs appear to be concentrated under the shrubs. *Thelypodium sagittatum* (Nutt.) Endl. is, perhaps, the most prominent in this latter habitat.

6. Rabbitbrush association
(*Chrysothamnetum nauseosi*)

The principal dominants of this association are two kinds of rabbitbrush, *Chrysothamnus nauseosus* var. *consimilis* (Greene) H. M. Hall and *C. nauseosus* var. *hololeucus* (Greene) H. M. Hall. The community is not common in the region and seems to be successional in nature. It has been observed occupying drained or disturbed land. The two principal varieties are present on the recently exposed gravel beaches at Pyramid Lake where they are associated with *Distichlis stricta, Echinopsilon hyssopifolius, Salsola kali* var. *tenuifolia, Heliotropium curassavicum* var. *oculatum* (Heller) Johnston, and other species of a more or less transitory nature in succession.

7. Iodinebush association
(*Allenrolfeetum occidentalis*)

This association is usually represented only by scattered plants of the iodinebush, *Allenrolfea occidentalis* (S. Wats.) Kuntze. Occasionally, saltgrass, *Distichlis stricta,* forms an herbaceous synusia between the bushes. At one station where 25 quadrats of 9 square meters each were laid out, iodinebush showed a total coverage of about 6 per cent of the area with a density of 0.7 plants per square meter.

The usual location for the iodinebush association is on a terrace adjacent to and from 5 to 10 feet below a big greasewood community. These terraces appear to be the result of wave erosion of the sediments under big greasewood when the playa-lake is at an unusually high level. The surface soil in the Allenrolfeetum, unlike that in the Sarcobatetum, usually stays wet all summer. A small soil well in a stand of this type revealed a friable crust to about 5 centimeters, followed by a wet clay which in turn was underlain at about 20 centimeters by a heavy, wet subsoil of prismatic clay. Analysis of the surface soil showed a pH of 8.8 and a soluble salt content 3½ times greater than that of any big greasewood surface soil tested.

8. SAMPHIRE ASSOCIATION
(*Salicornietum rubrae*)

Soils which are strongly saline and wetter than those under iodinebush provide the environment for an annual community dominated by *Salicornia rubra* A. Nels. The Salicornietum usually forms a prominent zone along the edges of small channels of water running into a playa. These streams are outlined in the autumn by the samphire's brilliant red. The individuals are usually very close together and, therefore, rather small. A series of 10 quadrats, each enclosing 1 square decimeter, evenly spaced throughout a stand of samphire revealed that the stocking was at the astounding rate of 13,570 plants per square meter at maturity.

9. ALKALI-GRASS ASSOCIATION
(*Puccinellietum fasciculatae*)

The alkali-grass association is characteristic of highly saline soils which are shallowly covered during most of the growing season by small ponds of still water. Sometimes, it occurs as a zone in the shallower channels just inside the Salicornietum. The typical situation shows tussocks of *Puccinellia fasciculata* (Torr.) Bicknell scattered rather openly and evenly through a small, shallow, saline pond.

10. SALTGRASS ASSOCIATION
(*Distichletum strictae*)

The dominant plant of this association, *Distichlis stricta*, apparently is able to tolerate a wide range of conditions. As a result, this community may be found on almost any saline soil except the very driest. Extensive stands occur in the shallow water around the edges

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of some of the more permanent playa-lakes. It may also occur along the more shallow flowing channels. From these locations, the long rhizomes spread out in all directions and establish the plant on the relatively dry saline soil of the banks. At Pyramid Lake, saltgrass is abundant as an invader of the recently exposed beach sands and gravels. In big greasewood stands adjacent to bare playas, saltgrass may be present as an herbaceous synusia. The *Distichlis stricta* union, thus, may exist as a unistratal association or represent the herbaceous layer in a multistratal association. In addition to the dominant species, *Distichlis dentata* Rydb. is sometimes present.

11. BULRUSH ASSOCIATION
(*Scirpetum*)

Emergent plants belonging to the genus Scirpus constitute almost the whole of the bulrush association. Present in varying degrees of abundance are *Scirpus americanus* Pers., *S. chilensis* Nees. and Mey., *S. paludosus* A. Nels., and *S. acutus* Muhl. At any one location, usually only one of the species is present in pure stand. Further investigations of the growth requirements of the species may reveal more than one association dominated by Scirpus. Some species seem to prefer running water, while others are most common in quiet, brackish water. Strictly speaking, the term "tule" should be applied to plants of this genus only. In western Nevada, however, the term is loosely applied to any narrow-leaved emergent vegetation and in this paper, emergent tule associations will include the Typhetum and Eleocharetum in addition to the Scirpetum.

12. CAT-TAIL ASSOCIATION
(*Typhetum*)

The Typhetum in the Carson Desert region seems to be dominated almost entirely by *Typha angustifolia* L. It occurs principally in deeper water than does the Scirpetum. Like that association, it covers many square miles in the region especially around Carson Sink and in the region of the Stillwater Slough. The abundance of cat-tail in the region has led to investigation of the areas as a possible source of down ("typha") to replace kapok in various uses.

13. SPIKE-RUSH ASSOCIATION
(*Eleocharetum*)

Spike-rush, mainly *Eleocharis macrostachya* Britton, occasionally

forms pure stands in shallow water. It is particularly abundant in old ditches.

14. COTTONWOOD ASSOCIATION
(*Populetum Fremontii*)

The cottonwood association is the only arborescent community to enter the Carson Desert region below 6,000 feet. The Populetum forms galeria forests along the lower Truckee, Carson, and Walker Rivers. In places, these groves may be almost a mile in width although usually they are not more than a few hundred feet across. The dominant stratum is occupied by a union consisting entirely of *Populus Fremontii* S. Wats. Two shrubby unions are usually present; a Salix union immediately adjoining the river shore and the *Artemisia tridentata* union over much of the flood-plain. The herbaceous vegetation, because of continuously available fresh water, is relatively luxuriant. It consists of a number of species of perennial grasses and other herbs. Much of this type is now under cultivation or in grazing.

15. SAGEBRUSH ASSOCIATION
(*Artemisietum tridentatae*)

The sagebrush association is typical of the semi-arid steppe country surrounding the Carson Desert on the west and north and on the higher mountains to the east. The Artemisietum does, however, enter the region concerned in this paper under two circumstances. In its typical form, the sagebrush association replaces the little greasewood-shadscale association above the highest Lahontan beach on the hills in the northwestern part of the region. Here, it is the climatic climax under precipitation in excess of 7 inches per year. The line between the little greasewood-shadscale type on the Lahontan sediments and the sagebrush association on the hills is sometimes quite sharp in that part of the Carson Desert area. In places on the west side of Pyramid Lake where the precipitation is adequate, the Artemisietum may come down on the rather thin Lahontan gravels of the steep slopes of that vicinity. An occasional individual of *Juniperus utahensis* (Engelm.) Lemmon may also appear there with sagebrush. The second type of occurence of this community in the Carson Desert is along the lower flood-plains of the rivers in places either too dry or possibly too saline for *Populus Fremontii*.

Since the sagebrush association is more typical of areas outside the Carson Desert region, a detailed analysis of the community will not

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be presented in this paper. It will suffice to describe the association in general terms. On the residual soils of the hills where the sagebrush association is the climatic climax, the Artemisietum consists of three unions. The frutescent union is characterized by *Artemisia tridentata, Tetradymia glabrata, Ephedra viridis* Coville, *Grayia spinosa, Purshia tridentata* (Pursh) DC., *Ribes velutinum* Greene, *Chrysothamnus puberulus* (D. C. Eaton) Greene, and *Chrysothamnus nauseosus* (Pall.) Britton. The perennial union exhibits several bunch-grasses and numerous forbs. Characteristic of this synusia are *Sitanion hystrix, Poa secunda* Presl., *Delphinium Andersonii* A. Gray, *Zygadenus venenosus* S. Wats., and numerous others. The composition of the original annual union in this community is somewhat difficult to determine because of the present dominance in that stratum of the introduced *Bromus tectorum* and *Bromus rubens*. The abundance of these two species is due, in part, to repeated range fires in the region caused primarily by the very presence of the bromes themselves. The great amount of combustible material produced by these two species creates a considerable fire hazard in this association during the dry summers. The fires tend to eradicate the native perennial herbaceous and woody vegetation leaving almost pure stands of Bromus over considerable areas. It seems safe to say that *Amsinckia tessellata* A. Gray, *Collinsia parviflora* Dougl., *Mimulus montioides* Gray, and *Phacelia adenophora* J. T. Howell are at least prominent members of the native annual union in the sagebrush association.

CLIMAX RELATIONS

Figure 4 illustrates, in a general way, the topographic and geologic relationships of the principal plant associations of the Carson Desert region. On the broad, dry plains of the Lahontan sediments and on the residual soils of the lower mountain ranges in the southern part of the region, the little greasewood-shadscale association appears to be the climatic climax. The climate of the little greasewood-shadscale association is warmer and distinctly drier than that of the Artemisietum. The normal precipitation of the Sarcobatetum Baileyi ranges from 4 to 6 inches, 50 to 75 per cent of the minimum required by sagebrush when not supplied by underground water. In the slightly cooler and more moist northwestern part of the region, the lower elevational limit of the sagebrush community on upland soils more or less coincides with the highest level reached by Lake Lahontan. Postclimax sagebrush and post-climax cottonwood enter the desert along
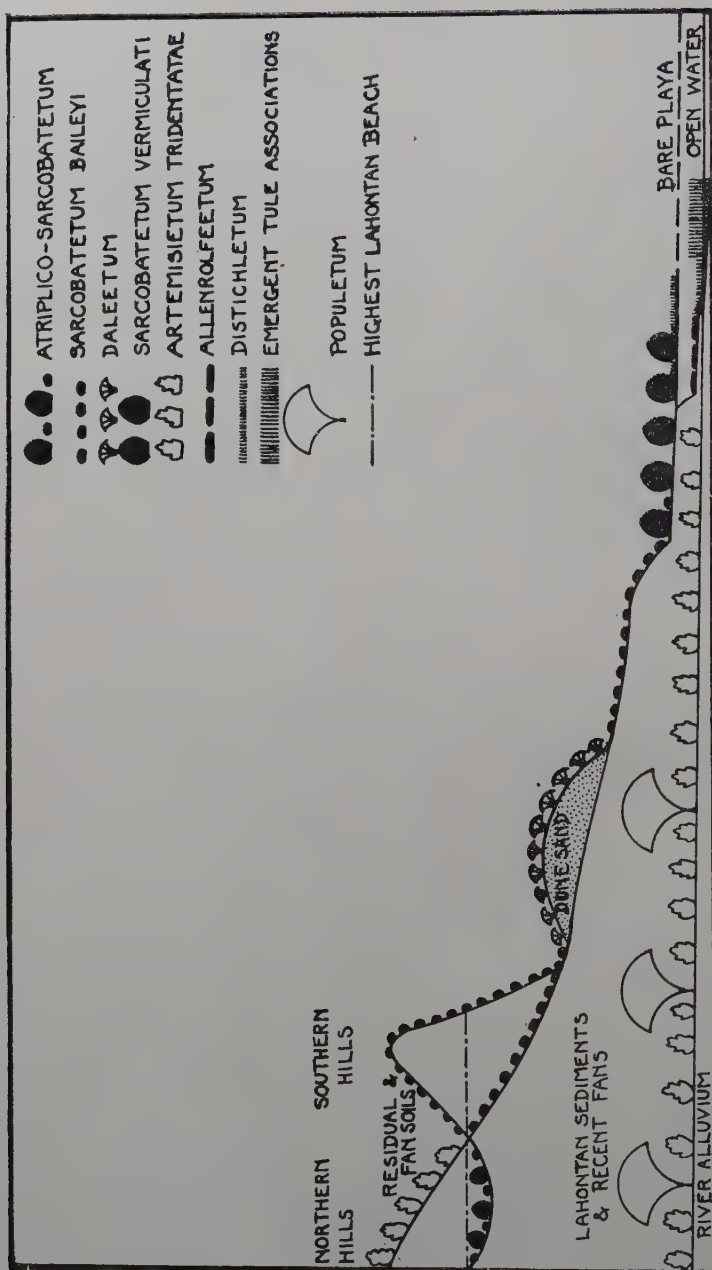
Figure 4. Diagrammatic representation of the topographic and geologic positions of the principal associations in the Carson Desert region.

NORTHERN HILLS
SOUTHERN HILLS

RESIDUAL & FAN SOILS
LAHONTAN SEDIMENTS & RECENT FANS
RIVER ALLUVIUM
DUNE SAND
BARE PLAYA
OPEN WATER

●●● ATRIPLICO-SARCOBATETUM
●●● SARCOBATETUM BAILEYI
🍂 DALEETUM
🌱 SARCOBATETUM VERMICULATI
🌿 ARTEMISIETUM TRIDENTATAE
━━━ ALLENROLFEETUM
▊▊▊▊ DISTICHLETUM
⌣ EMERGENT TULE ASSOCIATIONS
⌣ POPULETUM
───── HIGHEST LAHONTAN BEACH

the rivers where the fresh water table is close enough to the surface to supply water throughout the dry season. The dalea association on dune sands and the big greasewood and other stable associations on saline playa clays evidently represent edaphic climaxes. It is difficult, however, to see how the vegetation and soils in these situations can change in the direction of the climatic climax under the present arid climate and interior drainage conditions.

SUMMARY

1. Fifteen associations are described in a phytosociological analysis of the vegetation of the Carson Desert region, an area of microthermal arid climate in western Nevada.

2. Particular emphasis is placed upon the frutescent associations. The little greasewood-shadscale association on Lahontan sediments and residual soils, the dalea association on aeolian sand, the big greasewood association and the big greasewood-shadscale association on saline clays are quantitatively analyzed at a number of stations.

3. The little greasewood-shadscale association is considered to be the climatic climax on normal soils in this region where the precipitation is too low for the development of the sagebrush association.

ACKNOWLEDGMENTS

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STATION LOCATIONS

LITTLE GREASEWOOD-SHADSCALE ASSOCIATION

Sta. 1. 4.7 miles northeast of Hazen along power line.
Sta. 2. Adjoining Ft. Churchill at foot of Churchill Butte.
Sta. 3. 15.6 miles south of Fallon.
Sta. 4. 9.2 miles southeast of Fernley, on bench just west of Black Butte.
Sta. 5. 10.1 miles northeast of Fernley.
Sta. 6. 18.5 miles south of Fallon in Desert Mountains.
Sta. 7. 5.2 miles north of Schurz, south slopes of Desert Mountains.
Sta. 8. 3.5 miles north of Wabuska, Desert Mountains.
Sta. 9. 3 miles west of Sand Springs, just north of Eight-mile Flat.
Sta. 10. 5 miles southwest of Pyramid Lake, near Pyramid Mining Dist. 3 road.
Sta. 12. 6 miles north of Schurz in Desert Mountains.

DALEA ASSOCIATION

Sta. 1. Just west of Letteville, north side of Carson River.
Sta. 2. 4.2 miles northeast of Fernley.
Sta. 3. 5.7 miles northeast of Fernley.
Sta. 4. 10.9 miles northeast of Hazen along power line.
Sta. 5. 18 miles north of Schurz in Desert Mountains.
Sta. 6. 16 miles north of Schurz in Desert Mountains.
Sta. 7. 3 miles west of Sand Springs, just north of Eight-mile Flat.
Sta. 8. 2 miles west of Letteville, north side of Carson River.
Sta. 9. 1 mile north of Wadsworth.
Sta. 10. 5.2 miles northeast of Fernley.

BIG GREASEWOOD ASSOCIATION

Sta. 1. 1.4 miles east of Stillwater.
Sta. 2. Immediately southeast of Hazen.
Sta. 3. 8.7 miles northeast of Fernley in Hot Springs Flat.

BIG GREASEWOOD-SHADSCALE ASSOCIATION

Sta. 1. Roundhole Ranch, edge of Smoke Creek Desert.
Sta. 2. 8 miles southwest of Pyramid Lake, Cottonwood Creek Sink.

TABLE I

Species of the Sarcobatetum Baileyi listed in decreasing order of presence at ten stations.

SHRUBS	1	2	3	4	5	6	7	8	9	10
Sarcobatus Baileyi Coville.	x	x	x	x	x	x	x	x	x	x
Atriplex confertifolia (Torr. & Frém.) S. Wats.	x	x	x	x	x	x	x	x	x	x
Artemisia spinescens D. C. Eaton.	x	x	x		x	x	x	x	x	x
Eurotia lanata (Pursh) Moq.		x		x	x	x				x
Lycium Cooperi A. Gray.	x		x			x	x		x	
Opuntia pulchella Engelm.	x	x							x	
Dalea polyadenia Torr.	x	x								
Ephedra nevadensis S. Wats.		x				x				
Opuntia erinacea Engelm.		x						x		
Sarcobatus vermiculatus (Hook.) Torr.					x					
Tetradymia spinosa Hook. & Arn.					x					
Hymenoclea fasciculata A. Nels.						x				
Tetradymia glabrata A. Gray.							x			
Grayia spinosa (Hook.) Moq.										x
Artemisia tridentata Nutt.										x
PERENNIAL HERBS										
Sphaeralcea ambigua subsp. monticola Kearney.		x	x	x		x	x	x	x	x
Oryzopsis hymenoides (Roem. & Schult.) Ricker.		x				x	x	x		x

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TABLE I (Continued)

Species of the Sarcobatetum Baileyi listed in decreasing order of presence at ten stations.

	1	2	3	4	5	6	7	8	9	10
Hermidium alipes S. Wats.	x	x		x		x		x		
Hilaria Jamesii (Torr.) Benth.						x		x		
Rhysopterus corrugatus (Jones) Coulter & Rose.							x			
Lygodesmia grandiflora (Nutt.) Torr. & Gray.									x	
Astragalus iodanthus S. Wats.										x
Stipa speciosa Trin. & Rupr.										x
Sitanion hystrix (Nutt.) J. G. Smith.										x
ANNUAL HERBS										
Cryptantha circumscissa (Hook. & Arn.) Johnston.	x	x	x	x		x	x	x	x	x
Eriogonum vimineum Dougl.		x		x		x		x		x
Glyptopleura marginata D. C. Eaton.			x	x				x	x	x
Bromus rubens L.			x		x	x		x		x
Cryptantha micrantha (Torr.) Johnston.	x	x					x	x		
Oenothera clavaeformis Torr. & Frém.		x				x		x	x	
Oenothera contorta Dougl.			x	x					x	x
Festuca octoflora Walt. and var. hirtella Piper.			x			x		x		x
Gilia leptomeria A. Gray.							x	x	x	x
Abronia turbinata Torr.		x					x		x	
Descurainia californica (A. Gray) O. E. Schulz.			x			x				x
Cryptantha pterocarya (Torr.) Greene.				x				x		x
Eriogonum pusillum Torr. & Gray.							x		x	x
Bromus tectorum L.		x			x					x
Streptanthella longirostris (S. Wats.) Rydb.		x							x	
Eriogonum angulosum Benth.				x					x	
Coldenia Nuttallii Hook.				x			x			
Lepidium flavum Torr.						x		x		
Euphorbia ocellata var. arenicola (Parish) Jepson.						x			x	
Nama aretioides (H. & A.) Brand.							x			x
Erodium cicutarium (L.) L'Her.								x		x
Amsinckia tesselata A. Gray.								x		x
Descurainia sp.		x								
Gilia floccosa A. Gray.			x							

TABLE I (Continued)

Species of the Sarcobatetum Baileyi listed in decreasing order of presence at ten stations.

	1	2	3	4	5	6	7	8	9	10
Cryptantha sp.				x						
Caulanthus pilosus S. Wats.						x				
Dondia nigra (Raf.) Standl.					x					
Oenothera chamaenerioides A. Gray.						x				
Amsinckia sp.?							x			
Oenothera deltoides var. Piperi Munz.							x			
Astragalus sp.							x			
Tripterocalyx crux-maltae (Kellogg) Standl.							x			
Plagiobothrys Harknessii (Greene) Nels. & Macbr.								x		
Mentzelia albicaulis Dougl.								x		
Cleome sp.								x		
Blepharidachne Kingii (S. Wats.) Hack.								x		
Astragalus diphysus A. Gray.									x	
Chaenactis stevioides Hook. & Arn.										x
Malacothrix glabrata A. Gray.										x
Eriogonum sp.?										x
Descurainia paradisa (Nels. & Kenn.) O. E. Schulz.										x
Descurainia sophia (L.) Webb.										x
Gilia polycladon Torr.										x

TABLE II

Quantitative composition of the frutescent (dominant) stratum of the Sarcobatetum Baileyi at five stations. All figures based on 25 quadrats of 9 square meters each at each station. f = frequency, d = density per square meter, c = percentage coverage of total area, pc = percentage of total shrubby cover.

SPECIES		1	2	3	4	5
Sarcobatus Baileyi	f	92	100	100	96	88
	d	.35	.33	.51	.26	.15
	c	3.24	5.36	6.88	4.32	3.48
	pc	54.36	53.49	58.01	56.54	67.97
Atriplex confertifolia	f	96	84	100	92	76
	d	.21	.28	.82	.46	.19
	c	1.12	1.52	2.24	3.32	1.20
	pc	18.79	15.17	18.88	43.46	23.45

TABLE II—(Continued)

Quantitative composition of the frutescent (dominant) stratum of the Sarcobatetum Baileyi at five stations. All figures based on 24 quadrates of 9 square meters each at each station. f = frequency, d = density per square meter, c = percentage coverage of total area, pc = percentage of total shrubby cover.

Species		1	2	3	4	5
Artemisia spinescens	f	68	96	100		28
	d	.22	.97	1.53		.08
	c	.76	3.08	2.72		.12
	pc	12.75	30.74	22.93		2.34
Lycium Cooperi	f	48		12		
	d	.22		.01		
	c	.72		.02		
	pc	12.08		.16		
Dalea polyadenia	f	8				
	d	.01				
	c	.12				
	pc	2.01				
Ephedra nevadensis	f		4			
	d		.01			
	c		.04			
	pc		.40			
Eurotia lanata	f		8			40
	d		.01			.09
	c		.02			.20
	pc		.20			3.90
Sarcobatus vermiculatus	f					8
	d					.02
	c					.12
	pc					2.34

TABLE III

Quantitative composition of the herbaceous unions of the Sarcobatetum Baileyi at ten stations in 1941. All figures based on 25 quadrats of 1/5 square meter each at each station. f = frequency, d = density per square meter.

Perennials		1	2	3	4	5	6	7	8	9	10
Oryzopsis hymenoides	f		4				4	8			
	d		.2				.2	.6			
Sphaeralcea ambigua monticola	f						4	24		16	
	d						.2	1.2		1.0	
Astragalus iodanthus	f										4
	d										.2
Stipa speciosa	f										4
	d										.2

TABLE III (Continued)

Quantitative composition of the herbaceous unions of the Sarcobatetum Baileyi at ten stations in 1941. All figures based on 25 quadrats of 1/5 square meter each at each station. f = frequency, d = density per square meter.

ANNUALS		1	2	3	4	5	6	7	8	9	10
Cryptantha circumscissa	f	16	36					8	4	64	16
	d	1.0	3.2					.6	.2	12.2	2.4
Cryptantha micrantha	f	36						20			
	d	4.0						1.8			
Oenothera clavaeformis	f		4							4	
	d		.2							.2	
Eriogonum vimineum	f		8				4		4		52
	d		.4				.2		.2		6.8
Cryptantha sp.	f				8						
	d				.4						
Eriogonum angulosum	f				4					16	
	d				.2					1.2	
Descurainia californica	f						16				
	d						1.8				
Eriogonum pusillum	f							12		20	8
	d							.6		1.6	1.0
Amsinckia sp.?	f							4			
	d							.2			
Oenothera deltoides Piperi	f							4			
	d							.2			
Lepidium flavum	f								4		
	d								.2		
Erodium cicutarium	f								4		
	d								.2		
Bromus rubens	f								24		12
	d								2.2		.8
Astragalus diphysus	f									4	
	d									.2	
Streptanthella longirostris	f									4	
	d									.2	
Oenothera contorta	f									12	12
	d									1.6	.8
Gilia leptomeria	f									8	20
	d									.6	1.2
Bromus tectorum	f										8
	d										.4
Chaenactis stevioides	f										20
	d										2.0
Glyptopleura marginata	f										12
	d										1.0
Malacothrix glabrata	f										12
	d										.6

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TABLE IV

Species of the Daleetum listed in decreasing order of presence at ten stations.

Shrubs	1	2	3	4	5	6	7	8	9	10
Dalea polyadenia Torr.	x	x	x	x	x	x	x	x	x	x
Atriplex canescens (Pursh) Nutt.	x	x	x	x	x	x	x	x	x	x
Tetradymia glabrata A. Gray.	x	x	x	x	x	x	x	x	x	x
Tetradymia comosa A. Gray.	x	x	x		x	x	x	x	x	x
Sarcobatus Baileyi Coville.	x	x	x	x			x	x	x	x
Eurotia lanata (Pursh) Moq.	x			x				x	x	x
Opuntia pulchella Engelm.	x					x	x	x		
Atriplex confertifolia (Torr. & Frém.) S. Wats.		x		x						x
Artemisia spinescens D. C. Eaton.		x								x
Grayia spinosa (Hook.) Moq.							x		x	
Tetradymia spinosa Hook. & Arn.		x								
Hymenoclea fasciculata A. Nels.				x						
Ephedra nevadensis S. Wats.				x						
Perennial Herbs										
Oryzopsis hymenoides (Roem. & Schult.) Ricker.		x	x	x	x	x	x	x	x	x
Sphaeralcea ambigua subsp. monticola Kearney.	:	x		x	x	x	x			
Pentstemon acuminatus Dougl.	x				x	x	x	x		
Rhysopterus corrugatus (Jones) Coulter & Rose.	x					x		x		x
Lygodesmia grandiflora (Nutt.) Torr. & Gray.	x						x			
Rumex venosus Pursh.					x		x			
Hermidium alipes S. Wats.		x								
Annual Herbs										
Coldenia Nuttallii Hook.	x	x	x	x	x	x	x	x	x	x
Abronia turbinata Torr.	x	x	x	x	x	x	x	x	x	x
Cryptantha circumscissa (Hook. & Arn.) Johnston.	x	x	x		x	x	x	x	x	x
Gilia leptomeria A. Gray.	x	x	x	x		x	x	x	x	x
Euphorbia ocellata var. arenicola (Parish) Jepson.	x	x	x		x	x	x	x		x
Oenothera deltoides var. Piperi Munz.	x	x	x		x	x	x	x	x	
Cryptantha micrantha (Torr.) Johnston.	x		x		x	x	x	x	x	x
Eriogonum pusillum Torr. & Gray.	x	x	x	x			x	x	x	x
Phacelia bicolor Torr.	x		x		x	x	x	x	x	x
Tripterocalyx crux-maltae (Kellogg) Standl.	x	x			x			x	x	x

TABLE IV (Continued)

Species of the Daleetum listed in decreasing order of presence at ten stations.

SHRUBS	1	2	3	4	5	6	7	8	9	10
Nama aretioides (H. & A.) Brand.	x				x		x	x	x	
Mentzelia albicaulis Dougl.		x	x					x	x	x
Malacothrix sonchoides (Nutt.) Torr. & Gray.			x				x	x	x	x
Oenothera clavaeformis Torr. & Frém.		x	x	x			x			
Bromus tectorum L.			x				x		x	x
Streptanthella longirostris (S. Wats.) Rydb.			x		x		x		x	
Glyptopleura marginata D. C. Eaton.	x					x			x	
Salsola kali var. tenuifolia Tausch.		x	x							x
Chaenactis Xantiana A. Gray.			x						x	x
Oryctes nevadensis S. Wats.			x				x			x
Eriogonum vimineum Dougl.			x			x				x
Oenothera contorta Dougl.					x		x	x		
Bromus rubens L.						x	x		x	
Lupinus intermontanus Heller.							x		x	x
Astragalus diphysus A. Gray.	x						x			
Chenopodium leptophyllum Nutt.			x							x
Eriogonum angulosum Benth.			x						x	
Descurainia californica (A. Gray) O. E. Schulz.					x				x	
Plagiobothrys Harknessii (Greene) Nels. & Macbr.					x				x	
Descurainia longipedicellata (Fourn.) O. E. Schulz.					x	x				
Malacothrix glabrata A. Gray.									x	x
Cryptantha sp.		x								
Nama depressum Lemmon.					x					
Festuca octoflora Walt. and var. hirtella Piper.						x				
Gilia floccosa A. Gray.							x			
Helianthus anomalus Blake.							x			
Chenopodium sp.									x	
Franseria acanthicarpa (Hook.) Coville.									x	
Cleome lutea Hook.									x	

TABLE V

Quantitative composition of the frutescent (dominant) stratum of the Daleetum at seven stations. Figures for first three stations based on 25 quadrats of 4 square meters each; figures for remaining four stations based on 25 quadrats of 9 square meters each.

SPECIES		1	2	3	4	8	9	10
Dalea polyadenia	f	60	44	52	84	100	64	84
	d	.27	.26	.23	.27	.52	.16	.25
	c	9.48	3.84	5.72	3.32	9.60	2.88	3.10
	pc	33.52	39.83	23.87	31.92	84.51	24.44	39.00
Atriplex canescens	f	52	24	56	12	8	48	4
	d	.20	.06	.18	.01	.01	.07	.004
	c	8.64	1.12	3.68	.48	.10	2.00	.04
	pc	30.55	11.61	15.35	4.61	.88	17.24	.54
Tetradymia comosa	f	12	4	32			72	4
	d	.06	.01	.14			.11	.004
	c	3.00	.20	13.48			5.08	.30
	pc	10.60	2.07	56.26			43.79	3.77
Sarcobatus Baileyi	f	24	44	16	12	8	36	40
	d	.16	.39	.04	.02	.01	.04	.08
	c	7.16	3.68	.68	.76	.10	1.14	2.10
	pc	25.31	38.17	2.83	7.30	.88	9.83	26.40
Tetradymia glabrata	f			4	4	4	4	28
	d			.01	.004	.004	.004	.06
	c			.40	.08	.04	.10	1.94
	pc			1.66	.76	.35	.86	24.40
Eurotia lanata	f				92	96	36	4
	d				.26	.34	.06	.004
	c				1.40	1.52	.30	.01
	pc				13.46	13.38	2.59	.13
Atriplex confertifolia	f		4					8
	d		.03					.01
	c		.20					.14
	pc		2.07					1.76
Hymenoclea fasciculata	f				92			
	d				.30			
	c				4.20			
	pc				40.38			
Ephedra nevadensis	f				8			
	d				.01			
	c				.16			
	pc				1.53			
Grayia spinosa	f						12	
	d						.01	
	c						.10	
	pc						.86	

TABLE V (Continued)

Quantitative composition of the frutescent (dominant) stratum of the Daleetum at seven stations. Figures for first three stations based on 25 quadrats of 4 square meters each; figures for remaining four stations based on 25 quadrats of 9 square meters each.

SPECIES		1	2	3	4	8	9	10
Artemisia spinescens	f							20
	d							.05
	c							.32
	pc							4.02

TABLE VI

Quantitative composition of the herbaceous unions of the Daleetum at ten stations in 1941. All figures based on 25 quadrats of 1/5 square meter each at each station. f = frequency, d = density per square meter.

PERENNIALS		1	2	3	4	5	6	7	8	9	10
Oryzopsis hymenoides	f		8	4	8	48	24	4	24	44	44
	d		.4	.2	.6	3.0	3.6	.2	1.2	3.2	2.8
Sphaeralcea ambigua monticola	f					28	8				
	d					1.8	.4				
Pentstemon acuminatus	f	8				8	64				
	d	.4				.4	4.2				
ANNUALS											
Coldenia Nuttallii	f		52	80		48	8	28	56	76	88
	d		5.8	14.4		4.8	.4	2.0	10.8	14.8	10 0
Cryptantha circumscissa	f			48		60	80	68	96	88	48
	d			3.8		7.2	16.8	9.4	25.6	19.0	3.4
Abronia turbinata	f	8	4	4		4		16	8	4	16
	d	.4	.2	.2		.2		.8	.4	.2	.8
Gilia leptomeria	f		20	40	4		4	92		4	40
	d		1.6	3.2	.2		.4	23.2		1.4	4.0
Euphorbia ocellata arenicola	f	4	4	8			4		8		4
	d	.2	.2	.4			.2		.4		.2
Cryptantha micrantha	f	4		4			16	44	28	12	
	d	.2		.2			1.2	3.0	3.0	.8	
Phacelia bicolor	f			8		8	12	28	8	36	
	d			.4		.4	.6	1.8	.4	2.0	
Salsola kali tenuifolia	f		20	8							32
	d		1.4	.6							1.6
Cryptantha sp.	f		4								
	d		.2								
Mentzelia albicaulis	f		4						4	4	28
	d		.2						.2	.2	1.6
Tripterocalyx crux-maltae	f		4								
	d		.2								

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TABLE VI (Continued)

Quantitative composition of the herbaceous unions of the Daleetum at ten stations in 1941. All figures based on 25 quadrats of 1/5 square meter each at each station. f = frequency, d = density per square meter.

		1	2	3	4	5	6	7	8	9	10
Eriogonum pusillum	f			12	16			8	32	24	
	d			.8	.8			.6	1.6	1.4	
Chaenactis Xantiana	f			4							20
	d			.2							1.0
Bromus tectorum	f			20						28	36
	d			1.4						2.8	2.0
Oryctes nevadensis	f			4							8
	d			.2							.6
Eriogonum vimineum	f			8							4
	d			.8							.2
Chenopodium leptophyllum	f			8							4
	d			.4							.2
Streptanthella longirostris	f			4		4				12	
	d			.2		.2				.6	
Malacothrix sonchoides	f			8						12	12
	d			.6						.6	.6
Nama aretioides	f				20		4		4		
	d				1.6		.2		.2		
Oenothera deltoides Piperi	f					4					
	d					.2					
Oenothera contorta	f						4	4			
	d						.2	.2			
Astragalus diphysus	f						4				
	d						.2				
Eriogonum angulosum	f						4				
	d						.2				
Chenopodium sp.	f								4		
	d								.2		

TABLE VII

Quantitative composition of the frutescent (dominant) stratum of the Sarcobatetum vermiculati at three stations.

SPECIES		1	2	3
Sarcobatus vermiculatus (Hook.) Torr.	d	.59	.105	.07
	c	24.00	6.75	3.80
	pc	100.0	100.0	95.0
Atriplex lentiformis Torreyi (S. Wats.) H. & C.	d			.004
	c			.20
	pc			5.0

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TABLE VIII

Quantitative composition of the frutescent strata of the Atriplico-Sarco-batetum at two stations.

Species		1	2
Sarcobatus vermiculatus	d	.41	.38
	c	19.04	13.17
	pc	63.05	42.80
Atriplex lentiformis Torreyi	d	.23	.48
	c	6.24	8.64
	pc	20.66	28.07
Artemisia spinescens	d	.34	.51
	c	.92	4.00
	pc	3.05	13.00
Atriplex confertifolia	d	.44	.29
	c	2.76	3.42
	pc	9.14	11.11
Tetradymia spinosa	d	.14	.08
	c	.60	.94
	pc	1.99	3.05
Grayia spinosa	d	.08	.03
	c	.40	.60
	pc	1.32	1.95
Eurotia lanata	d	.11	
	c	.16	
	pc	.53	

TABLE IX

Soil characteristics at representative locations in the principal associations.

Location	Soil type	% Rock Greater Than 2 mm.	% Sand	% Silt	% Clay	% Total "Colloids"	pH	Conductance of solution as K x 10⁵
Bare region—Eight-mile Flat								
0—2 cm.	Clay	0	41.3	28.4	30.4	35.7	9.6	5006.2
25 cm.	Clay loam	0	39.3	34.4	26.4	32.7	9.6	2053.8
50 cm.	Sandy clay loam	0	63.3	14.4	22.4	26.7	9.6	1780.0
Sarcobatetum vermiculati—Sta. 2								
0—2 cm.	Silt loam	0	19.4	76.0	4.6	46.6	8.5	1128.2
30 cm.	Silty clay	0	7.4	59.0	33.6	85.6	8.6	843.2
50 cm.	Clay	0	9.1	23.6	67.3	77.9	9.0	801.0
Sarcobatetum vermiculati—Sta. 3								
0—2 cm.	Sand	0	85.3	8.7	6.0	8.4	9.4	315.4
25 cm.	Clay	0	13.3	20.0	66.7	76.7	9.1	272.4
50 cm.	Clay	0	31.3	24.4	44.4	56.7	9.4	161.8
Atriplico—Sarcobatetum—Sta. 1								
0—2 cm.	Sandy loam	0	60.6	24.7	14.7	21.4	7.3	22.3
30 cm.	Clay	0	45.6	12.0	42.4	46.4	9.1	66.4
Sarcobatetum Baileyi—Sta. 3								
0—2 cm.	Sand	24.9	82.1	15.0	2.9	4.9	7.7	16.4
30 cm.	Sandy clay loam	17.6	61.4	17.6	20.9	25.6	8.9	48.3
50 cm.	Sandy loam	0	71.4	18.6	9.9	12.5	9.0	89.6
100 cm.	Clay loam	3.9	49.8	25.6	24.6	28.2	8.9	295.2

TABLE IX (Continued)

Soil characteristics at representative locations in the principal associations.

Location	Soil type	% Rock Greater Than 2 mm.	% Sand	% Silt	% Clay	% Total "Colloids"	pH	Conductance of solution as K × 10^5
Sarcobatetum Baileyi—Sta. 4								
0—2 cm.	Sand	12.5	83.7	13.0	3.3	7.3	9.4	92.6
30 cm.	Sandy loam	10.0	64.7	21.0	14.3	18.3	8.9	18.7
50 cm.	Sandy loam	2.9	58.7	34.0	7.3	11.3	9.4	46.8
100 cm.	Silt loam	0	17.1	79.0	3.9	3.9	8.5	326.9
Sarcobatetum Baileyi—Sta. 12*								
0—2 cm.	Sand	18.0	83.1	13.6	3.3	4.9	7.8	13.2
30 cm.	Sand	7.0	85.1	9.6	5.3	7.9	7.9	12.0
50 cm.	Sand	4.4	90.7	6.0	3.3	5.3	8.0	11.3
Daleetum—Sta. 3								
0—2 cm.	Sand	0	95.1	3.6	1.3	1.9	7.3	30.1
25 cm.	Sand	0	95.1	3.6	1.3	2.9	7.4	3.6
50 cm.	Sand	0	95.1	3.6	1.3	2.9	7.4	3.3
100 cm.	Sand	0	92.1	4.6	3.3	3.9	9.1	15.4
Daleetum—Sta. 8								
0—2 cm.	Sand	0.4	95.4	3.6	0.9	0.9	7.4	94.4
30 cm.	Sand	0.8	94.4	4.0	1.6	1.6	7.9	16.2
50 cm.	Sand	0	94.4	4.6	0.9	1.6	7.8	13.5
100 cm.	Sand	0	98.4	1.0	0.6	0.6	8.0	13.7
Daleetum—Sta. 9								
0—2 cm.	Sand	0.8	93.4	5.0	1.6	3.6	7.2	5.3
30 cm.	Sand	1.1	90.4	6.0	3.6	4.6	7.0	4.8
50 cm.	Sand	1.0	88.8	5.6	5.6	7.2	7.0	6.0

* This station of the Sarcobatetum Baileyi is located on residual volcanic soil at an elevation of 4850 feet in the Desert Mountains. No vegetational analyses other than presence are available for this station at present.

THE CHARACEAE OF INDIANA—A PRELIMINARY REPORT*

By FAY KENOYER DAILY
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It has been demonstrated by others that the study of algae of Indiana in general has been neglected. In 1929 in an introduction to a classified check list of the algae of Indiana, Dr. C. M. Palmer (5) remarked, "Few papers have been published giving the names of the algae of Indiana." Also in 1932 after giving a phycological history of Indiana, Dr. B. H. Smith (7) observed, "This review of literature shows very clearly the meager amount of work which has been done on the algae in the state since the beginning fifty-five years ago." These statements are especially true of the Characeae, during the study of which group Dr. B. W. Everman and H. W. Clark (3) noted, "Indeed there have been so few workers in the field and relatively little material collected over the country generally that classification is exceedingly difficult." This statement was made almost twenty-five years ago, but the same condition still exists.

Recently a study of the Characeae of Nebraska was made by Dr. Walter Kiener (4) and the author (2). Dr. Kiener made an important contribution in collecting many new specimens from that state, and he also made available herbarium specimens located at the University of Nebraska. After a study of the available material, a key and descriptions were published. An attempt is now being made by the author to make a similar taxonomic study of the Characeae of Indiana. One hundred and ten specimens have been assembled and identified, but it is desirable to have considerably more before attempting to prepare a key and descriptions. Since there is a wide divergence in form with many intermediates within some species of the Characeae, and since the division of these species complexes into new species, varieties and forms seems to have caused a great deal of confusion in the past, the present paper uses only the species complex name in such instances. Further division may be made at a later date if deemed justifiable in the light of future study.

The three-fold purpose of this paper, then, is to report the data concerning collections made in Indiana which have not already been published; to make an appeal for any specimens of the Characeae now extant; and to stimulate the collection of new material.

Concerning the latter, it might be well to make a few comments upon collection of this group. The plants are generally found in ponds and lakes or sluggishly flowing streams. They are usually growing in less than ten feet of water and quite often are about the edge of the water upon the moist soil of the shore. The whole plant should be obtained if it can be reached from the shore or by wading. This includes the rhizoidal portion which must be obtained by digging it out of the mud. This is not always possible, however, because some of the plants may be reached only by use of a "Chara rake" similar to the one recommended by Nordstedt (in Allen, 1). After collection, the material should be washed gently to free it from debris, and should be laid out on paper to dry. Crowding should be avoided when arranging the collection as some of the more brittle forms are crushed by grinding of stem against stem if they are overlapped a great deal. Specimens may be dried by first pressing the material lightly for a short time to somewhat flatten the mount and then storing in a warm, airy place to dry rapidly. However, they may be placed in a drier used for the flowering plants if too much pressure is not applied to cause collapse of the cortex in the corticated forms. The Nitelleae are best prepared by floating out the more delicate forms on suitable paper and covering with cotton cloth or wax paper. To speed drying, when using the latter, all excess moisture should be removed by blotting lightly.

If it were more convenient for the collector, any of the usual laboratory reagents for preserving the algae, such as two per cent formalin, etc., could be used. However, one disadvantage of this method is that usually one can only make small collections. The color and natural appearance of such collections are also impaired, making the material less desirable for herbarium mounts when finally dried. The chief advantage of this method is that tissue is preserved in a more natural state for microscopic examination. If too much pressure and heat are avoided in the former method, however, it is preferred as the tissue will resume its normal condition when soaked in water or vinegar or any other suitable dilute acid usually used in removing the lime on incrusted forms.

In reporting the new collections below, the herbaria in which they may be found are indicated as follows :—BU, Butler University ; CM, Chicago Natural History Museum ; IU, Indiana University ; DU, DePauw University. (Duplicates of some collections are available for further distribution.)

When specimens are listed as "probably" *C. contraria,* etc., this means that the condition of the material is such that complete observations were impossible. However, enough characteristics have been observed to be reasonably sure of the identification.

The author wishes to acknowledge the aid of Dr. Ray C. Friesner for making available the facilities of the Butler University Botany Department; Dr. Francis Drouet of the Chicago Natural History Museum, Dr. Charles C. Deam of Bluffton, Indiana, Dr. Winona H. Welch of DePauw University, Dr. Naomi Mullendore of Franklin College, and Miss Rosalie Weikert of the New York Botanical Garden for the loan or gift of specimens ; Dr. C Mervin Palmer, Dr. John E. Potzger, and Mr. William A. Daily, all of Butler University, for many kindnesses rendered.

NITELLA

Nitella flexilis Ag. MARION COUNTY : Fall Creek Water Works, Indianapolis, *C. M. Palmer Id. 18,* Apr. 26, 1931 (BU) ; probably *N. flexilis,* in a large pond near Keystone av. and Fall creek, Indianapolis, *W. A. Daily,* Mar. 15, 1941 (CM, BU), *W. A. Daily, F. K. Daily, F. Drouet, E. R. Hupp, C. M. Palmer 929,* Aug. 16, 1942 (CM, BU), *W. A. & F. K. Daily 40* Oct. 25, 1942 (BU). STEUBEN COUNTY : Margin of Lake James, *W. H. Welch,* July 18, 1935 (DU, BU).

Nitella opaca Ag. WAYNE COUNTY : Drainage ditch (by N. S. road), Elliott's Mills Bog south of Richmond, *L. J. King 384,* May 11, 1941 (CM, BU).

CHARA

Chara aspera Willd. (Nearest var. *Macounii* Allen or *Chara Macounii* Allen as Robinson, 6, considered it). KOSCIUSKO COUNTY : Abundant in Beaver Dam lake, *W. A. Daily 79,* June 10, 1939 (CM, BU).

Chara Brittonii Allen. (As nearly as it has been possible to determine, this species has been known until the present only from the type specimen.) LA PORTE COUNTY : In standing water forming a "mat" on the surface, Mill Creek Bog, Mill Creek, *W. A. Daily 89,*

July 22, 1939 (BU). Randolph county: Raised bog along Highway 1 where it crosses Cabin creek 6.3 mi. north of Modoc, in water from second artesian well, *J. E. Potzger,* July 22, 1944 (BU), *R. C. Friesner, J. E. Potzger, W. A.* & *F. K. Daily 48,* Sept. 2, 1944 (BU).

Chara contraria A. Br. Bartholomew county: Probably *C. contraria* in ponds near overpass on Highway 31, north of Columbus, *W. A.* & *F. K. Daily 32,* Oct. 11, 1942 (BU). Cass county: Quarry west of Logansport on U. S. Highway 24, *W. A.* & *F. K. Daily 39,* Sept. 10, 1942 (BU). DeKalb county: In Indian lake, sec. 29, 2 mi. west of Corunna, *C. C. Deam 52272,* July 13, 1932 (IU, BU). Elkhart county: Probably immature *C. contraria,* St. Joseph river near Bristol, *C. C. Deam 55184,* July 18, 1934 (IU, BU). Fulton county: Probably *C. contraria,* abundant in 6 ft. of water, Lake Manitou, *C. C. Deam 56495,* Aug. 8, 1935 (IU, BU). Hancock county: Drainage ditch in Carlisle muck area 2 mi. north and 1.5 mi. east of Eden, *R. C. Friesner 18600,* Aug. 5, 1944 (BU). Jasper county: Common in old channel of the Kankakee river north of Tefft, *C. C. Deam 42227,* Aug. 19, 1925 (IU, BU). Johnson county: *N. Mullendore,* July 12, 1937 (BU). Kosciusko county: In 3 feet of water in outlet of Tippecanoe lake, *C. C. Deam 49265,* in 2½ ft. of water, *C. C. Deam 49276,* July 24, 1930 (IU, BU); in 1½ ft. of water in the Tippecanoe river at the outlet of Tippecanoe lake, *C. C. Deam 49283,* July 24, 1930 (IU, BU); Big Tippecanoe lake, Oswego, *W. H. Welch 2096,* July 20, 1935 (DU); not abundant, Loon lake adjoining Silver Lake Bog, Silver Lake, *W. A. Daily 78,* June 10, 1939 (CM, BU). Lagrange county: In ditch beside tamarack swamp and road, very abundant, on Road 20 about 7 mi. west of county line, *C. M. Palmer B 1028,* July 29, 1933 (BU). Lake county: Slough at Pine, *O. E. Lansing Jr. 1718,* June 4, 1903 (CM); in drainage ditch along U. S. Highway 12 near boundary of Lake county and Porter county, *D. Richards 190,* July 14, 1939 (CM). Marion county: Aquarium in Conservatory of Jordan Hall, Butler University, Indianapolis, *C. M. Palmer Id. 146,* Aug. 1930 (BU); probably *C. contraria,* Ind. State Fish Hatchery, Indianapolis, *C. M. Palmer Id. 78,* Aug. 4, 1931 (BU); swampy pool north of Broad Ripple and just east of interurban tracks and College av., south of White river, *C. M.* & *S. M. Palmer B 147,* Oct. 18, 1934 (BU); in large pond near Fall creek at Keystone av., Indianapolis, *W. A.* & *F. K. Daily, F. Drouet, E. R. Hupp,* & *C. M. Palmer 930,* Aug. 1942 (BU); ponds at Keystone and Fall creek, Indianapolis, *F. Drouet,*

C. M. Palmer, E. R. Hupp, W. A. & F. K. Daily 41, 42, Aug. 15, 1942 (BU) ; Emerald pool, John Holliday Park, Indianapolis, *C. T. Kenoyer, W. A. & F. K. Daily 1,* Sept. 27, 1942 (BU) ; Trout pool, John Holliday Park, Indianapolis, *C. T. Kenoyer, W. A. & F. K. Daily 2,* Sept. 27, 1942 (BU) ; in ponds at Keystone av. and Fall creek, Indianapolis, *W. A. & F. K. Daily 18,* Oct. 25, 1942 (BU) ; second pool at Goodman's Estate in Crow's Nest, Indianapolis, *H. T. Smolenski, W. A. & F. K. Daily 3,* Aug. 21, 1943 (BU) ; bridge pool, Goodman's Estate in Crow's Nest, Indianapolis, *H. T. Smolenski, W. A. & F. K. Daily 4,* Aug. 21, 1943 (BU) ; Trout pool, Goodman's Estate in Crow's Nest, Indianapolis, *H. T. Smolenski, W .A. & F. K. Daily 6,* Aug. 21, 1943 (BU) ; in pond at Marian College, Indianapolis, *C. T. Kenoyer, W. A. & F. K. Daily 29,* Oct. 17, 1943 (BU) ; at bridge over White river north of Broad Ripple on State Road 431 at city limit, the American Aggregate Gravel Pit, *W. A. & F. K. Daily 27,* May 1, 1944 (BU) ; Seventy-third st. near Keystone av., Indianapolis, old gravel pit pond near road at Builder's Sand & Gravel Co., *W. A. & F. K. Daily 19,* July 9, 1944 (BU). MARSHALL COUNTY: East side of Lake of the Woods, *C. C. Deam 49255,* July 23, 1930 (IU, BU). NOBLE COUNTY : With *C. fragilis,* shallow water east side of Bear lake, *C. C. Deam 47576,* Aug. 7, 1929 (IU, BU) ; in shallow water in Bear lake, *C. C. Deam 49385,* Aug. 14, 1930 (IU, BU). PORTER COUNTY: Shallow slough at Dune Park, *A. Chase,* Sept. 1, 1902 (CM) ; in dredge ditch 1 mi. south of Hebron, *C. C. Deam 42270,* Aug. 20, 1925 (IU, BU). PUTNAM COUNTY: Along Raccoon creek in stagnant pool, *E. J. Grimes 802,* Sept. 10, 1911 (DU). RANDOLPH COUNTY: Probably *C. contraria,* first artesian well in bog 6.3 mi. north of Modoc south of Cabin creek, *R. C. Friesner, J. E. Potzger, W. A. & F. K. Daily 43,* Sept. 2, 1944 (BU). SHELBY COUNTY: In gravel pit at Shelbyville, *F. K. & W. A. Daily 888,* Aug. 31, 1941 (CM, BU) ; Burnside Gravel Pit at Shelbyville, *W. A. & F. K. Daily 38,* Oct. 11, 1942 (BU), *25,* Oct. 3, 1943 (BU). STEUBEN COUNTY: In outlet of Crooked lake, *C. C. Deam,* June 17, 1903 (DU, BU) ; in ditch about ¼ mi. east of Hogback lake, *C C. Deam 1258,* July 24, 1906 (DU, BU) ; probably *C. contraria* at edge of Reed lake about 1½ mi. northwest of Reed Lake, *C. C. Deam 14381,* July 5, 1914 (DU, BU) ; shallow water near bank of Bass lake, *C. M. Palmer B 1008,* July 28, 1933 (BU) ; sandy north shore of Fox lake, 1½ mi. southwest of Angola, *C. M. Palmer B 1017,* July 28, 1933 (BU) ; probably *C. contraria* attached and floating at edge of Failing lake

north of Angola, *C. M. Palmer B 1020, B 1021, B 1024,* July 28, 1933
(BU) ; with *C. fragilis* at bottom in 8 in. of water along margin of
Crooked lake, *C. M. Palmer 1190,* Sept. 30, 1933 (BU) ; in 6 ft. of
water in Hamilton lake at Hamilton, *C C. Deam 56684,* Aug. 20, 1935
(IU, BU). WAYNE COUNTY: In shallow and deeper water at edge
of Lake Wehi, *W. A. & F. K. Daily 16,* July 16, 1944 (BU) ; in small
stream in shallow sluggish water, 5 mi. north of Hagerstown, 0.3 mi.
along Road 1 from junction with 35, *R. C. Friesner, J. E. Potzger,
W. A. & F. K. Daily 56,* Sept. 2, 1944 (BU). WHITLEY COUNTY:
Probably *C. contraria* submerged in water at northeast border of
Shriner lake, *C C. Deam 14575,* Aug. 24, 1914 (DU, BU) ; Loon lake,
C. C. Deam 49403, Aug. 14, 1930 (IU, BU) ; in old lake, *C. C. Deam
49427 B,* Aug. 14, 1930 (IU, BU).

Chara coronata Ziz. MARTIN COUNTY: In creek near Indian
Springs, *C. C. Deam 43493,* July 23, 1926 (IU, BU). PORTER COUN-
TY: With *C. contraria,* shallow slough, Dune Park, *A. Chase,* Sept.
1, 1902 (CM, BU) ; shallow slough, Dune Park, *A. Chase 1984,* Sept.
1, 1902 (CM, BU).

Chara foetida A. Br. CARROLL COUNTY: 5½ mi. south of Norway
Dam on east bluff fed by springs, *W. A. Daily 12,* July 28, 1938
(BU). KOSCIUSKO COUNTY: In ditch in gravel pit north of Winona,
C. C. Deam 1497, Aug. 17, 1906 (DU, BU). LAGRANGE COUNTY:
In gravel pit along Pigeon river about 3 mi. southeast of Mongo,
E. B. Williamson, Oct. 21, 1928 (IU, BU) ; at edge of Pigeon river
pool above and below water level, *C. M. Palmer B 56,* Oct. 1, 1933
(BU). LAKE COUNTY: Wolf lake near Hammond, *N. Mullendore
123,* 1923. RANDOLPH COUNTY: Growing on wet peat near top of
elevated bog on south side of Cabin creek at junction with Road 1, 6.3
mi. north of Modoc, *R. C. Friesner 18501,* July 22, 1944 (BU) ; from
first artesian well in bog 6.3 mi. north of Modoc south of Cabin creek,
R. C. Friesner, J. E. Potzger, W. A. & F. K. Daily 45, 46, Sept. 2,
1944 (BU). ST. JOSEPH COUNTY: On mud bottom of spring near
St. Joseph river south of St. Mary's College, Holy Cross, *D. Parker,
E. M. Reed, D. Richards,* and *J. C. Strickland 583,* May 11, 1940 (CM,
BU). TIPPECANOE COUNTY: Near mouth of Tippecanoe river at
Hog Point, *C. C. Deam 17710,* July 20, 1915 (DU, BU). WAYNE
COUNTY: In small stream in shallow sluggish water 5 mi. north of
Hagerstown, 0.3 mi. along Rd. 1 from junction with 35, *R. C. Fries-
ner, J. E. Potzger, W. A. & F. K. Daily 55,* Sept. 2, 1944 (BU).

Chara fragilis Desv. BARTHOLOMEW COUNTY: In ponds near

overpass on Highway 31 north of Columbus, *C. T. Kenoyer, W. A. & F. K. Daily 22*, Sept. 19, 1943 (BU); probably *C. fragilis,* ponds near overpass on Highway 31 north of Columbus, *C. T. Kenoyer, W. A. & F. K. Daily 26,* Sept. 19, 1943. DECATUR COUNTY: In water at edge of Lake McCoy, *W. A. & F. K. Daily 28, 36,* Oct. 11, 1942 (BU). HAMILTON COUNTY: Fox Prairie Bog, *R. Prettyman,* June 19, 1937 (BU). MARION COUNTY: Small stream on Road 52, southeast part of county, *C. M. Palmer Id. 130,* June 25, 1932 (BU); driveway pool at Goodman's Estate in Crow's Nest, Indianapolis, *H. T. Smolenski, W. A. & F. K. Daily 5,* Aug. 21, 1943 (BU). NOBLE COUNTY: Shallow water east side of Bear lake, *C. C. Deam 47576,* Aug 7, 1929 (IU, BU). SHELBY COUNTY: Burnside Gravel Pit, Shelbyville, *W. A. & F. K. Daily 24,* Oct. 3, 1943 (BU). STEUBEN COUNTY: At bottom in 8 inches of water along lake margin, Crooked lake, *C. M. Palmer 1190,* Sept. 30, 1933 (BU); probably *C. fragilis* at lake margin not attached, Lake James, *C. M. Palmer B 29,* Sept. 30, 1933 (BU). UNION COUNTY: In about 6 ft. of water in old abandoned gravel pit, Robert's Pond, near Liberty, *A. & J. Ehlers* with *W. A. & F. K. Daily 17,* July 15, 1944 (BU). WAYNE COUNTY: In shallow water at edge of Lake Wehi, *W. A. & F. K. Daily 15,* July 16, 1944 (BU); with *C. contraria,* in shallow and deeper water at edge of Lake Wehi, *W. A. & F. K. Daily 16,* July 16, 1944 (BU).

Chara gymnopitys A. Br. CASS COUNTY: Moist soil and in water at edge of Lake Cicott, *W. A. & F. K. Daily 7, 10,* Sept. 9, 1942 (BU). LAKE COUNTY: Moist sandy soil of slough at Miller's near Lake Michigan, *C. C. Deam 21271,* Aug. 26, 1916 (DU, BU). LA PORTE COUNTY: Upon soil at the edge of water, Mill Creek Bog, Mill Creek, *W. A. Daily 90,* July 22, 1939 (BU). MORGAN COUNTY: In shallow water at pool's edge at Jewel lake at Bethany Park near Martinsville, *W. A. & F. K. Daily 37,* Sept. 20, 1942 (BU).

Chara gymnopus A. Br. BARTHOLOMEW COUNTY: In pond north of Columbus near overpass on Highway 31, *W. A. & F. K. Daily 33,* Oct. 11, 1942 (BU); in water trickling through grass near overpass on Highway 31 north of Columbus, *W. A. & F. K. Daily 35,* Oct. 11, 1942 (BU); ponds near overpass on Highway 31 north of Columbus, *C. T. Kenoyer, W. A. & F. K. Daily 20, 23,* Sept. 19, 1943 (BU). CASS COUNTY: In water at edge, Lake Cicott, *W. A. & F. K. Daily 12,* Sept. 9, 1942 (BU). JEFFERSON COUNTY: In pond along railway just north of North Madison, *C. C. Deam 56483,* Aug. 3, 1935 (IU, BU). LAKE COUNTY: In shallow water of Calumet river among

sand dunes north of Miller Station, *P. D. Voth & F. Drouet 2362,* Sept. 28, 1938 (CM). NOBLE COUNTY: In 2 ft. of water in Elkhart river just below Jones lake and just before Wallen lake, *students of Will Scott* (*C. C. Deam 6*), Aug. 25, 1930 (IU, BU). WHITLEY COUNTY: In old lake, *C. C. Deam 49427 A,* Aug. 14, 1930 (IU, BU).

Chara hydropitys Reich. LAKE COUNTY: Shallow sloughs, Pine, *E. J. Hill 141/1882,* Sept. 16, 1882 (CM). PORTER COUNTY: Shallow slough at Dune Park, *A. Chase 1983,* Sept. 1, 1902 (CM). WAYNE COUNTY: In shallow water of Lake Wehi, near Germantown, *W. A. & F. K. Daily 14,* July 16, 1944 (BU).

Chara sejuncta A. Br. PORTER COUNTY: Calumet river, Forsyth, *E. J. Hill 197/1880,* Sept. 18, 1880 (CM). SPENCER COUNTY: Artificial pond at Lincoln City, *C. C. Deam 22343,* Oct. 11, 1916 (IU, BU). STEUBEN COUNTY: In the outlet of Crooked lake, *C. C. Deam 20924,* Aug. 19, 1916 (IU, BU). SULLIVAN COUNTY: In old coal strip mine at margin of the water 5 mi. south of Sullivan, *C. M. Palmer B 25,* Sept. 7, 1933 (BU).

Chara verrucosa Itzig. NOBLE COUNTY: With *C. contraria* in shallow water in Bear lake, *C. C. Deam 49385,* Aug 14, 1930 (IU, BU).

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ADDITIONS TO THE FILAMENTOUS MYXO-PHYCEAE OF INDIANA, KENTUCKY AND OHIO[1]

By WILLIAM A. DAILY

The Eli Lilly Company

During the past several years, numerous specimens of the Myxophyceae from Indiana, Kentucky and Ohio have accumulated in the herbaria cited below. Some of these species presumably have not previously been reported for this region and are now placed on record.

It is known that many collections of algae, the bases for previous reports, have been lost or are inaccessible. It is the desire of the writer and of other students of the herbarium that all published works on the algae be based only upon permanently preserved specimens (represented in private and established herbaria).

I wish to acknowledge the generous aid of Dr. Francis Drouet in placing at my disposal the facilities of the Cryptogamic Herbarium of the Chicago Natural History Museum; of Dr. Ray C. Friesner for making available the facilities of the Botany Department of Butler University; and Dr. C. M. Palmer, and Fay K. Daily for kindnesses rendered.

Herbaria in which specimens cited are to be found are indicated by means of the following abbreviations: Da, Herbarium of W. A. Daily (on file in the Herbarium of Butler University); CM, Cryptogamic Herbarium, Chicago Natural History Museum; P, Herbarium of C. Mervin Palmer (on file in the Herbarium of Butler University).

Italicized collection numbers unless accompanied by the name of a collector are my own.

STIGONEMATACEAE

FISCHERELLA AMBIGUA (B. & F) Gom.—KENTUCKY: WOLFE COUNTY: On sandstone in Tight Hollow near Pine Ridge, *A. T. Cross, J. Tucker* & W. A. *Daily 773,* Sept. 1940 (Da, CM).

FISCHERELLA THERMALIS (B. & F.) Gom.—INDIANA: LA PORTE COUNTY: On soil in old fields east of Smith Station, 8 miles

north of La Porte, *P. D. Voth & F. Drouet 2438*, Oct. 1938 (Da, CM)

STIGONEMA MAMILLOSUM (Lyngb.) Ag. ex B. & F.—OHIO: HOCKING COUNTY: On sandstone, Cantwell Cliff State Park, *F. K. & W. A. Daily 686*, Aug. 1940 (Da, CM).

STIGONEMA MINUTUM (Ag.) Hass. ex B. & F.—KENTUCKY: POWELL COUNTY: On sandstone, Natural Bridge State Park, *F. K. & W. A. Daily 396*, June 1940 (Da, CM).

STIGONEMA PANNIFORME (Ag.) B. & F.—OHIO: CENTRAL PART: With *Schizothrix purpurascens* on dry prairie, *C. E. Taft*, 15 Oct. 1938 (CM).

HAPALOSIPHON PUMILUS (Kütz.) Kirchn. ex B. & F.—INDI-ANA: STEUBEN COUNTY: Attached and floating at margin of Failing lake, *C. M. Palmer B 1020*, 28 July 1933 (CM, P). Cited as *Oscillatoria geminata* Menegh. by C. M. Palmer, Butler Univ. Bot. Stud. 3: 103 April (1934).

NOSTOCACEAE

NOSTOC ELLIPSOSPORUM (Desmaz.) Rabenh. ex B. & F.—OHIO: HAMILTON COUNTY: On moist hard soil, Addyston ponds, Addyston, *L. Lillick 242*, 4 Aug. 1934 (CM); on damp soil, Hazelwood preserve, Cincinnati, *J. H. Hoskins & W. A. Daily 233b*, Nov. 1939 (CM). ATHENS COUNTY: From limestone rock on Wilson's farm near Athens, *135, 137*, 1939 (CM).

NOSTOC HUMIFUSUM Carm. ex B. & F.—KENTUCKY: TODD COUNTY: Pond on Russelville road 2 miles from Guthrie, *B. B. McInteer 573*, 15 Aug. 1929 (CM).

NOSTOC MACROSPORUM Menegh. ex B. & F.—INDIANA: JEN-NINGS COUNTY: With *Anacystis rupestris* on limestone in canyon, Muscatatuck State Park, Vernon, *F. K. & W. A. Daily 1106*, May 1942 (Da, CM). PARKE COUNTY: On moist sandstone cliff by Sugar creek northeast of Turkey Run Inn, *F. Drouet & D. Richards 2485*, 16 June 1939 (CM), on sandstone cliffs, Falls canyon, *F. Drouet & D. Richards 2474*, 16 June 1939 (CM).

NOSTOC PARMELIOIDES Kütz. ex B. & F.—INDIANA: JENNINGS COUNTY: Attached to limestone in stream above Hinchman's cave, Vernon, *58*, early spring, 1934 (Da, CM).

NODULARIA HARVEYANA (Thw.) Thur. ex B. & F.—INDIANA: MARION COUNTY: On wet mud in lane through Bacon's Swamp, Indianapolis, *C. M. Palmer, R. N. Webster, R. Prettyman, D. Webster & F. Drouet 2518*, 17 Aug. 1939 (P, CM).

ANABAENA CIRCINALIS (Kütz.) Rab. ex B. & F.—INDIANA: MARION COUNTY: Bloom in Fish Hatchery pond, Riverside, Indianapolis, *F. K. Daily,* 31 May 1941 (Da, CM).

ANABAENA OSCILLARIOIDES Bory ex B. & F.—KENTUCKY: WOLFE COUNTY: On wet sandy soil near Torrent, *R. Kosanke, F. K. & W. A. Daily 462,* July 1940 (Da, CM).

ANABAENA OSCILLARIOIDES var. STENOSPORA B. & F.—INDIANA: VIGO COUNTY: from a swamp in Otter township, Terre Haute, *H. H. Welch* 1, 9 Aug. 1940 (CM).

ANABAENA VARIABILIS Kütz. ex B. & F.—OHIO: COSHOCTON COUNTY: In ditch by Fresno road near N.A.E.W., *L. J. King 1026,* 30 May 1943 (CM), collected near the station, N.A.E.W., *L. J. King 1024,* May 1943 (CM).

ANABAENA SPIROIDES Klebahn—OHIO: HAMILTON COUNTY: Bloom in lake of the Church of the Little Flower, Cincinnati, *432,* July 1940 (Da, CM), bloom in pond of Lakeview fish hatchery, Cincinnati, *433,* July 1940 (Da, CM).

CYLINDROSPERMUM MAJUS Kütz. ex B. & F.—KENTUCKY: WOLFE COUNTY: On sandstone near Torrent, *R. Kosanke, F. K. & W. A. Daily 458,* July 1940 (Da, CM).

RAPHIDIOPSIS CURVATA Fritsch & Rich.—OHIO: MERCER COUNTY: With *Merismopoedia glauca,* Beaver creek near Celina, *J. B. Lackey,* Aug. 1940 (Da, CM). HAMILTON COUNTY: A bloom in Inwood Park lake, Cincinnati, *139,* Oct. 1939 (Da, CM). This species is distinguished by its evaginate and sharply pointed trichomes which are usually curved or spiraled.

RIVULARIACEAE

CALOTHRIX ADSCENDENS (Näg.) B. & F.—KENTUCKY: POWELL COUNTY: With *Scytonema Hofmannii* on limestone cliff near Slade, *A. T. Cross, J. Tucker & W. A. Daily 754,* Sept. 1940 (Da, CM).

CALOTHRIX BRAUNII B. & F.—INDIANA: MARION COUNTY: With *Amphithrix janthina* B. & F., on wood submersed in a small pond near Fall creek at Keystone ave., Indianapolis, *F. Drouet, E. R. Hupp, C. M. Palmer, F. K. & W. A. Daily 942,* 16 Aug. 1942 (Da, CM). JENNINGS COUNTY: Brownish coating on rock, *C. M. Palmer 155,* 24 Feb. 1934 (P, CM), from a rock in Vinegar Mills canyon in Muscatatuck State Park, Vernon, *20,* 30 April 1939 (Da, CM).

DICHOTHRIX BAUERIANA (Grun.) B. & F.—INDIANA: BAR-
THOLOMEW COUNTY: With *Schizothrix lardacea* Gom., on limestone
at water-line in quarry south of Scenic falls, Hartsville, *C. Kenoyer,*
F. K. & *W. A. Daily 1134,* 19 Sept. 1943 (Da, CM). SHELBY COUNTY:
With *Schizothrix laterita* Gom., on limestone in quarry No. 3 at water-
line and below near St. Paul, *F. K.* & *W. A. Daily 1141,* 3 Oct. 1943
(Da, CM).

DICHOTHRIX GYPSOPHILA (Kütz.) B. & F.—KENTUCKY: CAR-
TER COUNTY: With *Scytonema Myochrous* B. & F., on a limestone
cliff, Carter's Caverns, *L. Walp,* fall, 1940 (CM).

SCYTONEMATACEAE

HASSALLIA BYSSOIDEA (Berk.) Hass. ex B. & F.—OHIO: HOCK-
ING COUNTY: On rock, Cantwell Cliffs State Park, *F. K.* & *W. A.
Daily 686,* Aug. 1940 (Da, CM). WARREN COUNTY: On limestone
near Foster, *J. H. Hoskins* & *W. A. Daily 228,* Nov. 1939 (Da, CM).
SCIOTO COUNTY: On rocks along Spruce creek, *154,* Oct. 1939 (Da,
CM). VINTON COUNTY: On limestone, 5 miles east of McArthur,
125, Oct. 1939 (Da, CM).

SCYTONEMA CRUSTACEUM Ag. ex B. & F.—OHIO: ERIE COUNTY:
Quarry pool, Kelley's Island, *L. H. Tiffany,* 9 June 1931 (CM).

SCYTONEMA FIGURATUM Ag. ex B. & F.—OHIO: OTTOWA COUN-
TY: In Kelley Isle quarry, 1 mile west of Lakeside near Marblehead,
Catawba Island, *F. K.* & *W A. Daily 588,* July 1940 (Da, CM).
HIGHLAND COUNTY: With some *Scytonema alatum* B. & F., on Ce-
darville dolomite near Baker's Fork of Ohio Brush creek, near Fort
Hill, *A. T. Cross* & *J. Lambert,* Sept. 1941 (Da, CM). ADAMS COUN-
TY: On dolomite in falls below east side of Buzzard's Roost Rock,
146, Oct. 1939 (Da, CM). CHAMPAIGN COUNTY: With *Schizothrix
lacustris* Gom. & *Scytonema Myochrous,* Urbana Bog, *M. S. Markle
8,* 1938 (Da, CM). HAMILTON COUNTY: On the side-walls of Eden
Park reservoir, Cincinnati, *J. B. Lackey,* Sept. 1942 (CM).

SCYTONEMA HOFMANNII Ag. ex B. & F.—KENTUCKY: POW-
ELL COUNTY: With *Calothrix adscendens,* on limestone cliffs near
Slade, *A. T. Cross, J. Tucker* & *W. A. Daily 754,* Sept. 1940 (Da,
CM).

SCYTONEMA JAVANICUM Born. ex B. & F.—INDIANA: MARION
COUNTY: On side of flower pot in Pahud's greenhouse, Indianapolis,
F. K. & *W A. Daily 1177,* 20 May 1944 (Da, CM). OHIO: HAM-
ILTON COUNTY: On wet bricks in greenhouse, University of Cincin-

nati, Cincinnati, *267,* April 1940 (Da, CM); on rock in Eden Park Conservatory, Cincinnati, *181,* Oct. 1939 (Da, CM).

SCYTONEMA OCELLATUM Lyng. ex B. & F.—KENTUCKY: WOLFE COUNTY: On rock beneath falls, Torrent, *R. Kosanke, F. K. &W. A. Daily 496,* July 1940 (Da, CM).

OSCILLATORIACEAE

PORPHYROSIPHON NOTARISII (Menegh.) Kütz. ex Gom.—OHIO: ADAMS COUNTY: On soil in a prairie patch near Seaman, *289,* May 1940 (Da, CM). For a discussion of this species see F. Drouet, Amer. Jour. Bot. 24 (9): 601 (1937).

SCHIZOTHRIX FASCICULATA (Näg.) Gom.—INDIANA: STEUBEN COUNTY: Attached to submerged stones, Fox lake, *C. M. Palmer 152,* 28 July 1933 (P, CM). MARSHALL COUNTY: On stones near depot, Lake Maxinkuckee, *H. W. Clark & B. W. Evermann 250,* 30 Aug. 1906 (CM), near the shore at the depot, *H. W. Clark & B. W. Evermann 153,* 30 Oct. 1906 (CM).

SCHIZOTHRIX FUSCESCENS Kütz. ex Gom.—OHIO: OTTAWA COUNTY: In shallow water in Kelley Isle quarry, Marblehead, Catawba Island, *F. K. & W. A. Daily 583,* July 1940 (CM).

SCHIZOTHRIX LAMYI Gom.—OHIO: HAMILTON COUNTY: With *Schizothrix purpurascens,* on soil, Brickyard fish pond adjoining Arlington Cemetery, Cincinnati, *425,* July 1940 (Da, CM).

SCHIZOTHRIX LACUSTRIS A. Br. ex Gom.—OHIO: OTTAWA COUNTY: With *Nostoc Muscorum & Fischerella ambigua,* Marblehead quarry near Marblehead, Catawba Island, *F. K. & W. A. Daily 591 A,* July 1940 (Da, CM). CHAMPAIGN COUNTY: With *Scytonema figuratum & S. Myochrous,* Urbana Bog, *M. S. Markle 8,* 1938 (Da, CM), *J. H. Hoskins,* 1926 (Da, CM); with undeveloped *Scytonema Myochrous & S. figuratum, J. H. Hoskins,* 1926 (Da, CM).

SCHIZOTHRIX PULVINATA (Kütz.) Gom.—INDIANA: STEUBEN COUNTY: Fox lake, *C. M. Palmer 1019,* July 1933 (CM).

PLECTONEMA PURPUREUM Gom.—OHIO: WASHINGTON COUNTY: In a near-dry pool in Constitution, *H. Noland, F. K. & W. A. Daily 894,* Oct. 1941 (Da, CM).

PLECTONEMA ROSEOLUM (Richt.) Gom.—OHIO: HAMILTON COUNTY: In culture jar, University of Cincinnati greenhouse, Cincinnati, *740,* Sept. 1940 (Da, CM); dense mat on top of culture from University of Cincinnati greenhouse, Cincinnati, *L. Lillick 720,* 13 March 1935 (CM); dense mat on top of culture from University of

Cincinnati greenhouse, Cincinnati, *L. Lillick* & *I. Lee 614,* 2 March 1934 (CM).—This specimen is cited as *Oscillatoria terebriformis* Ag. by *L. Lillick* & *I. Lee,* Amer. Midl. Nat 15: 718 (1934). WASH-INGTON COUNTY: In a submerged gelatinous layer on sandstone rocks in the Hocking Sandstone quarry pond near Constitution, *H. Noland, F. K.* & *W. A. Daily 896,* Oct. 1941 (Da, CM).

PLECTONEMA TOMASINIANUM (Kütz.) Born. ex Gom.—INDI-ANA: MARION COUNTY: Fall Creek pumping station, Indianapolis, *C. M. Palmer 156,* July 1933 (P, CM). KOSCIUSKO COUNTY: Float-ing in canal near Warsaw, *C. M. Palmer Id. 173,* 23 Aug. 1935 (CM). STEUBEN COUNTY: With *Coelosphaerium Kuetzingianum,* floating at margin of Hog-back lake, *C. M. Palmer 150,* July 1933 (P, CM).

SYMPLOCA DUBIA (Näg) Gom.—KENTUCKY: POWELL COUN-TY: near Slade, *A. T. Cross, J. Tucker* & *W. A. Daily 761,* Sept. 1940 (Da, CM). OHIO: LORAIN COUNTY: On iron pipe in the Cleveland Sandstone quarry No. 6, South Amherst, *F. K.* & *W. A. Daily 607,* July 1940 (Da, CM). ATHENS COUNTY: In scum on sandstone near falls, Asylum ponds, Athens, *A. H. Blickle 3,* June 1941 (Da, CM).

SYMPLOCA ELEGANS Kütz. ex Gom.—KENTUCKY: POWELL COUNTY: On sandstone near tunnel on Sky Bridge road near Nada, *843,* Oct. 1940 (Da, CM).

LYNGBYA GUISEPPEI Drouet.—OHIO: ATHENS COUNTY: In shallow water, Wilson's farm near Athens, *128,* Oct. 1939 (Da, CM). See F. Drouet, Field Mus. Bot. Ser. 20: 135, pl. 2, f. 8. 1942.

LYNGBYA OCHRACEA (Kütz.) Thur. ex Gom.—OHIO: LORAIN COUNTY: With *Tribonema Bombycinum* in small pond in woods, east branch of Vermillion river, *P. Smith 26,* 20 April 1939 (CM).

LYNGBYA VERSICOLOR (Wartm.) Gom.—INDIANA: MARION COUNTY: Lakeside lake near New Augusta, *F. K.* & *W. A. Daily 1036,* Sept. 1942 (Da, CM). ST. JOSEPH COUNTY: In shallow water of Lake Marion, St. Mary's College, Holy Cross, *D. Parker,* 20 July 1940 (CM). MARSHALL COUNTY: Near depot grounds, Lake Max-inkuckee, *H. W. Clark* & *B W. Evermann 141,* 28 Aug. 1906 (CM), South end of Lake Maxinkuckee, *H. W. Clark* & *B. W. Evermann 71, 191, 262,* 11 Aug. 1906 (CM). KENTUCKY: CARTER COUNTY: On rocks in spray of water-fall at Carter caves, *D. Parker,* 16 May 1942 (CM).

PHORMIDIUM FAVOSUM (Bory) Gom.—INDIANA: JENNINGS COUNTY: In rapid stream, *C. M. Palmer 144,* Feb. 1934 (P). KEN-

TUCKY: MADISON COUNTY: With *Phormidium autumnale,* on wet overhanging rocks, Kentucky river near Richmond, *C. M. Palmer 40,* March 1932 (P, CM). BOONE COUNTY: On rock in rushing stream, *L. Lillick 61,* 7 April 1933 (CM), attached to rocks in stream, *L. Lillick 162, 7* April 1933 (CM). OHIO: ERIE COUNTY: Blue Hole of Castalia, Castalia, *F. K. & W. A. Daily 592,* July 1940 (Da, CM). ADAMS COUNTY: Light green mass attached to leaves and mud in swift flowing streams, *L. Lillick 100,* 29 April 1933 (CM). Thin mat on wet rocks in running water near Cincinnati, *L. Lillick* and *I. Lee 602,* 1932 (CM). In running water near Columbus, *W. A. Kellerman B 23,* 5 May 1892 (CM).

PHORMIDIUM LUCIDUM (Ag.) Kütz. ex Gom.—OHIO: HAMILTON COUNTY: On submerged mud in University of Cincinnati greenhouse, Cincinnati, *L. Lillick & I. Lee 611,* 3 Nov. 1933 (Da, CM).

PHORMIDIUM SETCHELLIANUM Gom.—INDIANA: CARROLL COUNTY: On sluiceway of Lake Shafer dam, Monticello, *867,* July 1941 (Da, CM). OHIO: ERIE COUNTY: From the Blue Hole of Castalia, Castalia, *F. K. & W. A. Daily 601,* July 1940 (Da, CM).

PHORMIDIUM SUBFUSCUM (Ag.) Kütz. ex Gom.—OHIO: HAMILTON COUNTY: On dam in Sharon Woods, Sharonville, *C. Botts, F. K. & W. A. Daily 302,* June 1940 (Da, CM).

OSCILLATORIA ARTICULATA Gardn.—INDIANA: STEUBEN COUNTY: With *Merismopoedia glauca,* stream east of Snow lake, *C. M. Palmer B 34,* Sept. 1933 (Da, CM). ST. JOSEPH COUNTY: On mud in pool, St. Mary's College, Holy Cross, *D. Parker, E. M. Reed, D. Richards & J. C. Strickland 584,* 11 May 1940 (CM). MARSHALL COUNTY: With *Anacystis peniocystis,* Lake Maxinkuckee, near the northwest shore by Culver, *H. W. Clark & B. W. Evermann 123,* 28 Aug. 1906 (CM). MARION COUNTY: On submerged mud, drainage ditch, *C. M. Palmer Id. 85,* 5 Aug. 1931 (CM).

OSCILLATORIA CORTIANA Menegh. ex Gom.—INDIANA: SHELBY COUNTY: In small pool in limestone quarry, St. Paul, *F. K. & W. A. Daily 879,* Aug. 1941 (Da, CM).

OSCILLATORIA CURVICEPS Ag. ex Gom.—INDIANA: MARION COUNTY: Floating in pools, Bacon's Swamp, Indianapolis, *C. M. Palmer, R. N. Webster, R. Prettyman, D. Webster & F. Drouet 2512,* Aug. 1939 (Da, CM, P), Fall creek and Keystone ave., Indianapolis, *F. Kenoyer & W. A. Daily 261,* Feb. 17, 1940 (Da, CM). GRANT COUNTY: Floating in masses, Lake Galatia near Fowlerton, *101,*

Aug. 1939 (Da, CM). KENTUCKY: KENTON COUNTY: South of Dudley Pike on Lexington road, south of Erlanger, *J. H. Hoskins & W. A. Daily 245,* Dec. 1939 (Da, CM) ; with *O. tenuis* & *Spirulinā major,* along creek on Lexington road, north of Erlanger, *J. H. Hoskins & W. A. Daily 246,* Dec. 1939 (Da, CM).

OSCILLATORIA PROLIFICA (Grev.) Gom.—KENTUCKY: FAYETTE COUNTY: Lexington, *B. B. McInteer,* (Da, CM). OHIO: HAMILTON COUNTY: Pond east of the mausoleum of Otto Armleder, Spring Grove cemetery, Cincinnati, *J. H. Hoskins* & *W. A. Daily 208,* Nov. 1939 (Da, CM)

OSCILLATORIA RUBESCENS D. C. ex Gom.—INDIANA: CASS COUNTY: With *Chroococcus limneticus, Coelosphaerium Kuetzingianum* & *Lyngbya Birgei,* Lake Cicott, *F. K.* & *W. A. Daily 1024,* 10 Sept. 1942 (Da, CM). SHELBY COUNTY: Planktonic in Burnsides Gravel pit, Shelbyville, *F. K.* & *W. A. Daily 1164, 1163,* Oct. 1943 (Da, CM). BARTHOLOMEW COUNTY: Planktonic in limestone quarry pit near Scenic falls, Hartsville, *C. Kenoyer, F. K.* & *W. A. Daily 1170,* 19 Sept. 1943 (Da, CM). LA PORTE COUNTY: South Pine lake, *M. E. Britton,* Aug. 1939 (CM).

OSCILLATORIA SANCTA var. CALDARIORUM (Hauck) Lagerh. ex Gom.—INDIANA: MARION COUNTY: A brownish black extensive layer on moist soil in Garfield Park conservatory, Indianapolis, *C. M. Palmer 47,* March 1932 (P, CM).

OSCILLATORIA TENUIS var. NATANS (Kütz.) Gom.—OHIO: As *Oscillaria natans?* Neils Run, *W. A. Kellerman E 23,* 29 April 1892 (CM).

OSCILLATORIA TENUIS var. TERGESTINA (Kütz.) Gom.—OHIO: HAMILTON COUNTY: Floating in clumps on pond in Spring Grove cemetery, Cincinnati, *266,* April 1940 (Da, CM).

A QUADRAT STUDY OF MELTZER WOODS, SHELBY COUNTY, INDIANA*

By CARL O. KELLER
Indianapolis Lutheran Schools

As one travels eastward on return from a trip through the prairie states, perhaps the most characteristic feature of the landscape which starts him humming the strains of, "Back Home Again in Indiana," are the beautiful woodlands along the highways of our state. These woodlands are remnants of the great Eastern deciduous forest upon which the pioneers gazed with amazement as they penetrated the interior of our continent. The botanist and Nature lover of the present day ofttimes wish they could have had the thrill of looking at the stately array of massive-trunked, majestic giants in that forest primeval. There are no quantitative data available to show just what the sociology of this forest was originally, but judging from the remnants of the ancient towering monuments found in some virgin forest areas by Butler ecologists (3, 11, 24), we may assume that trees from 150-200 feet tall with a girth of 20 feet or more were not uncommon. Early settlers and explorers with no particular botanical or ecological interest were impressed with the grandeur of the forest through which they traveled, as may be seen from their journals and other records. Ovid Butler (2) reports that Pierre Joseph Celoron de Blainville, who traveled down the Allegheny and Ohio rivers in 1749, dined one day with twenty-eight other men in a hollow sycamore somewhere in the Ohio Valley.

There were giants in those days, but, alas, most of them have fallen victim to the touch of Midas and have been converted into gold. Gold, of course, was what many of the early pioneers were seeking, and when they found that the natural resources of the northern part of the New World offered wealth in greater measure than the actual gold found by Cortez and Pizarro in the southern parts, they began to garner this wealth without restraint.

To the farmer, however, the forest presented a problem. Corn and produce could not be grown under the shading canopy of the

trees, or among their living roots. Clearing the land was a necessary operation if agriculture were to prosper, but the idea that the forests were inexhaustible, and could never be depleted, led to indiscriminate cutting and wasteful burning of timber just for the purpose of getting rid of it. Community log-rollings were quite common at this time, and all too frequently the only thing left from a pile of logs (worth hundreds of dollars today) would be enough ashes to make a batch of soap.

The early lumbermen and loggers also had the idea that this great source of wealth would never diminish. To use the words of Stewart H. Holbrook (6), to the early logger "a tree was something that contained so many thousand feet of boards, or, he might figure it to contain fully one quart of hard liquor. In any case, the tree was to be cut as quickly as possible. 'Let daylight into the swamp.'"

And when there was daylight everywhere in the swamps of Michigan and Wisconsin, when the valuable *Pinus strobus* and other coniferous timber had been practically depleted, then the hardwoods to the south came in for their share of the slaughter. Commercial interests have pillaged our Indiana forests to the extent that only in a few places in the state can one find small areas which have been protected from the axe of the lumbermen by far-sighted individuals who realized that the most rapid acquisition of money is not always the best and surest way to ultimate wealth. Such a man is Brady Meltzer, owner of the woods which we surveyed for this study. Like Joseph Cox, whose woods we studied in 1942 (14), Mr. Meltzer seemed to have a sort of tender affection for his trees. There were certain ones among them to which he pointed with particular pride, the most outstanding of which was a Shumard's red oak, 52 inches DBH., and a swamp white oak, 54 inches DBH. These two monarchs were not within our lines of survey, but their proud owner did not wish them to be overlooked, so taking a recess from his work in the field, he led us down the pasture lane to see "something worth looking at."

"There is some valuable timber in this woods," he said, as we walked back to the road, "and it would make a nice piece of farm land, if cleared, but our country needs forests, so I'm going to leave it alone." It is a rare pleasure to find such conservation-minded men who do not let their interest in getting all they can for themselves overshadow their consideration for our national welfare, and also the welfare of future generations. It is the hope of the writer that

Mr. Meltzer's woods, together with the other stands of virgin timber still left in Indiana, may long remain as a monument to the spirit of conservation ; and that students of ecology and forestry in generations to come may have access to these tracts as laboratories for scientific research, where they may find some new facts on successional trends by comparing their findings with those recorded by us of the present generation. The survey for this study was made March 27, 1943.

LOCATION OF THE MELTZER WOODS

The Meltzer woods is located in Shelby County, Indiana, near the eastern boundary of the county, in Liberty Township, T. 12 N., R. 8 E., Section 8. It is about eleven miles west of the village of Milroy, and just north of state road 244. The area of the tract is about forty acres.

GEOLOGY AND PHYSIOGRAPHY

The southeastern two-thirds of Shelby County lies within the Muscatatuck Regional Slope, with altitude ranging from 650 to 920 feet above sea level, giving it a maximum relief of 270 feet.

According to Malott (8), the Muscatatuck Regional Slope is the most notable regional slope in the entire state. It merges rather indistinctly into the low-land area on the west and the glacial plain on the north. Shelby County lies at the northern edge of this region. It is within the boundaries of Illinois and Early Wisconsin glaciation, and is covered with a rather thin layer of glacial drift which rests upon a stratum of New Albany shale, underlain by bedrock of Devonian and Silurian limestones.

CLIMATIC FEATURES

Indiana is near the southern margin of the area having long, severe winters. Visher (16) gives the normal average January temperature as ranging from 33° F. in the southern part of the state to 25° in the north. Shelby county lies midway between these two extremes. It has a growing season of from 160 to 180 days. The average annual precipitation for most of the state is about 40 inches. This is fairly evenly distributed throughout the year. The air is generally moist, with relative humidity averaging about 70% during the day. At night the lower air becomes super-saturated and moderate to heavy dews result.

The average wind velocity for the state is about eight miles per hour, with southwest winds prevailing in summer and northwest winds in winter. Gales and tornadoes are rare, and when they do occur, only small areas are affected.

METHODS

The 100 square meter quadrat was used as a unit of sampling. The quadrats were laid out by means of a stout cord with loops ten meters apart. These loops were slipped over stakes to form the corners of the areas to be tabulated. Two lines of survey were laid out, since the mature part of the woods was not of sufficient depth to include fifty quadrats in a continuous line. It was not originally intended to make a comparative study of the two sectors, since from casual observation the existing differences were not strikingly apparent, but since the tabulations showed rather marked differences, it was decided to present it in this way. A ten-meter skip was left between each unit area, as well as between the two lines. DBH. measurements were taken with wooden calipers. All stems over one inch in diameter were measured and tabulated. All young trees less than one inch DBH., and a meter or more in height, were also counted. It is assumed that these stems give a better idea of the dynamics of reproduction in an area than the smaller seedlings, many of which do not survive their first winter.

OBSERVATIONS

There were 43 different woody species found in this survey. They distributed themselves into the following life forms: 22 tall trees, 7 small trees, 4 large shrubs, 6 small shrubs, and 4 lianas. 37 different species were found in each sector. Some found in one sector were not found in the other and vice versa. *Acer saccharum, Fraxinus americana,* and *Fagus grandifolia* totalled more than half the number of stems above one inch DBH. (table I). Basal area percentages (table II) show that *Fagus grandifolia* is the most prominent species in the stand, constituting 27.33% of the total basal area, while *Acer saccharum* constituted only 3.78%, but in comparing the percentages of total stems below one inch and those one to two inches DBH. (table I), it appears that *Acer saccharum* is gaining in prominence and *Fagus grandifolia* is on the decline. In the one to two-inch size-class we find the following distribution: *Acer saccharum,* 26.59%, and *Fagus grandifolia,* 10.71%. In the size-class below one

inch, *Acer* drops to 7.99% and *Fagus* to .86%. It should be pointed out, however, that in this size-class competition involves species of the shrub stratum, *Lindera benzoin*—42.62%; *Asimina triloba*—8.77%; besides the young of the dominants.

Fraxinus americana shows rather unusual prominence for a woods of this type (table II), represented by the following percentages: stems below one inch, 13.21%; one to two-inch stems, 22.62%; all stems above one inch, 20.39%; and total basal area, 10.57%. The mortality rate of this species here is apparently not so great as it was found to be in the Mauntel woods by Potzger and Friesner (12).

Other species represented by greater basal area percentages than *Acer saccharum* were: *Ulmus americana*, 12.51%; *Carya laciniosa*, 10.12%; *Quercus alba*, 10.08%; *Quercus borealis* var. *maxima*, 6.26%; and *Quercus bicolor*, 6.01%.

Only seven of the species showed a frequency index of more than 50% (table II). They were: *Fraxinus americana*, 98%; *Acer saccharum*, 88%; *Lindera benzoin*, 76%; *Asimina triloba*, 72%; and *Fagus grandifolia*, 70%. This compares favorably with the Cox woods (14) which showed the same number of species with a F. I. of 50% or more. In the Berkey woods, however, Potzger and Friesner (11) found only five species showing so high a rate of frequency.

Because of the large number of species participating in the crown cover, this can hardly be called a beech-maple woods as listed (type 57) by the American Society of Foresters (15). The writer is inclined to consider it in the same class as the Berkey woods (11), and classify it as mixed-mesophytic, the concept proposed by Miss Braun (1).

A striking difference was found in the sociological make-up of the two sectors surveyed. This was particularly apparent in comparing the status of the maples. In the south sector, *Acer saccharum* had a basal area of 1462.41 sq. in., against 368.37 in the north sector (table II). *Acer rubrum* had 3.93 sq. in. in the south sector against 14.14 in the north sector. The total basal area covered in the south sector was 31,061.73 sq. in., while that covered in the north sector was only 17,412.32 sq. in.

DISCUSSION

In an extensive study to determine what is climax in central Indiana, Potzger and Friesner (13) have concluded that the climate in this area favors a modified *Acer-Fagus* climax, and that microclimate,

introduced by topography, causes and maintains the *Quercus-Carya* cover type. They point out that the term *Acer-Fagus* must be made very inclusive of many other species playing a part in the crown cover when forests of this type are considered. Potzger (10), in his Monroe County study, considers the so-called *Acer-Fagus* association as more of a mixed hardwoods type with *Acer* and *Fagus* playing a prominent role. Braun (1) places the true *Acer-Fagus* association into the northern limits of the deciduous forest, and regards the *Acer-Fagus* association in Indiana as a "mixed mesophytic association."

The unusual prominence of *Fraxinus americana* in the Meltzer woods makes it considerably different from other forest areas in which *Fagus* is as prominent as here, but, as the Society of American Foresters Committee on Forest Types (15) suggest, there will always be areas which stand as transitions between existing types, and it cannot be expected that any type list suitable for a region the size of the eastern United States will provide a name for every combination. In this connection, Phillips (9) points out that a climax very rarely, if ever, is wholly uniform floristically and structurally, and that climax associations making up the climax formation show faciations and facies, lociations and locies, climatically determined, and serations edaphically determined. Cain (4) considers the factor of soil in the complexities of the climax, showing that through its physical structure and chemical composition it determines to a greater or less extent the life it bears. And to these factors should be added, also, the soil moisture conditions.

When considering each of the two sets of quadrats in this study separately, and comparing them, one is impressed with the differences caused by microclimatic and edaphic factors. Perhaps the greatest variation was found in the status of *Acer*. In the south sector *Acer saccharum* and *Acer negundo* were almost four times as important as they were in the north sector, while *Acer rubrum* showed the opposite ratio of importance. This observation is based on basal area rather than abundance, in agreement with the view of Cain (4) that dominance should be judged by the area, or space covered by the plants. Another prominent difference found in the two lines of survey was in the greater number of small stems in the north sector, and in the greater total basal area covered by those in the south sector.

Edaphic factors are, without doubt, exerting a decided control on the species participating with *Acer saccharum* and *Fagus grandifolia*

in the crown cover. *Carya laciniosa, Liquidambar styraciflua, Quercus bicolor, Ulmus spp.,* as well as the shrub *Lindera benzoin,* are representative of poorly drained habitats, at least habitats which are wet during the early part of the growing season. This apparently explains the status of *Acer saccharum* in the Meltzer woods. With increased drainage, *Acer saccharum* may replace most of the afore-mentioned species except *Fagus.* Then a mixed mesophytic forest deprived of strong representation by species typical of the transitional floodplain habitat may develop. Lee (7) shows a number of different stages in the development of the floodplain forest, varying with soil composition, soil moisture, and drainage. Friesner and Ek (5) found two distinctly different forest types within a small area in Shenk's woods, in Howard County. This difference was due primarily to a variation in soil moisture. Further research would be necessary to determine the cause of the variations found in the Meltzer woods, but it may be assumed that a series of soil-moisture studies would give some interesting data.

Inasmuch as the Meltzer Woods is sufficiently unique in character to place it in a class by itself, showing no very close comparison with any particular type, or with any other woods in Indiana that has come to our attention, we might conclude, as suggested in the introduction, that such an area should be set aside as a laboratory of research. Valuable and costly as lumber is at the present time, these trees will be more valuable to the conservation program of the United States in the future if left standing than they will be to commercial interests if they were cut down and sawed into boards.

SUMMARY

1. This paper presents a study of the Meltzer woods, Shelby County, Indiana, based on fifty 100-square-meter quadrats.

2. The study emphasizes the importance of conserving such unusual areas as laboratories for ecological and forest research.

3. Woody species were represented by twenty-two species of tall trees, seven small trees, four large shrubs, six small shrubs, and four lianas.

4. *Acer saccharum, Fraxinus americana,* and *Fagus grandifolia* make up 58% of the stems above one inch DBH. Fagus constitutes 27% of the total basal area.

5. *Acer saccharum* and *Fraxinus americana* have the greatest abundance in the smaller stems (with the exception of shrubby species). *Fagus grandifolia* is poorly represented in the small stem size-class, indicating a decline in rate of reproduction and survival.

6. The Meltzer woods is a somewhat unusual and complex part of the mixed mesophytic forest, representing a transitional stage between wet lowland forest and the ultimate climax in central Indiana under optimum mesophytic habitat conditions.

ACKNOWLEDGMENT

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TABLE I

Size—classes of various species in 50 quadrats. a—north sector (25 quadrats). b—south sector (25 quadrats).

Species		Below 1"	1"	2"	3-5"	6-10"	11-15"	16-20"	21-25"	26-30"	31-35"	36-40"	41-45"	46-50"	Total stems above 1"
Acer	a	9	3												3
negundo	b	13	9	2											11
A.	a	4	2		1										3
rubrum	b	3	1	1											2
A.	a	82	36	21	19	1									77
saccharum	b	114	43	34	22	3			1	1					104
Asimina	a	106	7												7
triloba	b	109	7	1											8
Carpinus	a	8	16	10	8										34
caroliniana	b	14	11	5	7	1									24
Carya	a	4	2												2
cordiformis	b	6	1						1						2
C. glabra	a	2													
C.	a	9	2					1	2	2					7
laciniosa	b	17	4	1	3	1	1	1	3	1					15
Celtis	a	2	2	1	1										4
occidentalis	b	7	3	1	3										7
Cercis	a														
canadensis	b		1												1
Cornus	a			2											2
florida	b	3													
Crategus spp.	a	6	2	3	1										6
	b	3	1		3										4
Evonymus	a														
atropurpurea	b	3	1												1
Fagus	a	13	20	15	9	2	4	9	7						66
grandifolia	b	8	11	8	1	1	7	10	7	1					46
Fraxinus	a	155	23	9	15	1							1	1	50
americana	b	169	52	30	17	1	3	1	3	1					108
F.	a														
nigra	b								1						1
Gleditsia	a														
triacanthos	b					1									1
Gymnocladus	a	4	1			1		1							3
dioica	b		1				1								2
Juglans	a	1	1												1
cinerea	b														
J.	a	2													
nigra	b								1						1
Lindera	a	380	20	1											21
benzoin	b	685													
Liquidambar	a	2			2					1					3
styraciflua	b	2				2				1					3

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TABLE I—(Continued)

Size—classes of various species in 50 quadrats. a—north sector (25 quadrats). b—south sector (25 quadrats).

Species		Below 1"	1"	2"	3-5"	6-10"	11-15"	16-20"	21-25"	26-30"	31-35"	36-40"	41-45"	46-50"	Total stems above 1"
Liriodendron	a	4	1	1	8	3									13
tulipifera	b	1			2		1		1			1			5
Morus	a	15	4												4
rubra	b	6		4	1										5
Ostrya	a	10	7	1	1										9
virginiana	b	1	1												1
Prunus	a	25	14	3	5		1								23
serotina	b	44	9		4										13
Quercus	a	2								1	1				2
alba	b						1					1		1	3
Q.	a	3					1								1
bicolor	b						1					1	1		3
Q. borealis	a	2	1	2							1				4
var. maxima	b	2	1		1						1		1		4
Rhus	a	202	1												1
toxicodendron	b	42													
Ribes	a	22													
americanum	b														
Rosa	a	4													
palustris	b														
Rubus	a														
allegheniensis	b	1													
R.	a	1													
occidentalis	b														
Sambucus	a														
canadensis	b	1													
Smilax	a	9													
hispida	b	1													
Campsis	a	5													
radicans	b														
Tilia	a	7	1	1			2			1					5
americana	b	13	3	1	3			1							8
Ulmus	a	6	4	1	3	1	2	1			1				13
americana	b	7		1		5	2		2		2	1			13
U.	a	19	3												3
fulva	b	11	3		1	1									5
Viburnum	a	19	2												2
prunifolium	b	17	3												3
Vitis	a	10	3												3
sp.	b	2													
Zanthoxylum	a	10													
americanum	b	4													

TABLE II

Showing percentages of small stems, total stems, basal areas and F. I. (a—north sector (25 quadrats) b—south sector (25 quadrats)

Species		Stems below 1" No.	%	Stems 1"—2" No.	%	Total stems No.	%	Basal areas sq. in.	%	F. I.
Acer	a	9	.78	3	1.21	3	.82	2.36	.01	28
negundo	b	13	1.00	11	4.29	11	2.72	13.35	.04	36
A.	a	4	.34	2	.81	3	.81	14.14	.08	12
rubrum	b	3	.23	2	.78	2	.49	3.93	.01	04
A.	a	82	7.05	57	22.98	77	20.81	368.37	2.11	88
saccharum	b	114	8.84	77	30.08	104	25.68	1462.41	4.71	88
Asimina	a	106	9.11	7	2.82	7	1.89	5.50	.03	68
triloba	b	109	8.46	8	3.12	8	1.98	8.64	.02	76
Carpinus	a	8	.69	26	10.48	34	9.19	117.02	.67	52
caroliniana	b	14	1.08	16	6.25	24	5.93	112.31	.36	36
Carya	a	4	.34	2	.81	2	.54	1.57	.01	16
cordiformis	b	6	.47	1	.39	2	.49	491.66	1.60	32
C.	a	2	.17	—	—	—	—	—	—	04
glabra	b	—	—	—	—	—	—	—	—	—
C.	a	9	.77	2	.81	7	1.89	2509.35	14.42	44
laciniosa	b	17	1.32	5	1.95	15	3.71	2394.68	7.71	60
Celtis	a	2	.17	3	1.21	4	1.08	17.28	.10	16
occidentalis	b	7	.54	4	1.56	7	1.73	44.77	.14	32
Cercis	a	—	—	—	—	—	—	—	—	—
canadensis	b	—	—	1	.39	1	.25	.78	—	04
Cornus	a	—	—	2	.81	2	.54	6.28	.04	04
florida	b	3	.23	—	—	—	—	—	—	04

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TABLE II—(Continued)

Showing percentages of small stems, total stems, basal areas and F. I. a—north sector (25 quadrats) b—south sector (25 quadrats)

Species		Stems below 1" No.	%	Stems 1"—2" No.	%	Total stems No.	%	Basal areas sq. in.	%	F. I.
Crategus	a	6	.52	5	2.02	6	1.62	30.63	.18	20
spp.	b	3	.23	1	.39	4	.99	32.99	.11	24
Evonymus	a	—	—	—	—	—	—	—	—	—
atropurpurea	b	3	.23	1	.39	1	.25	.78	—	08
Fagus	a	13	1.12	35	14.11	66	17.84	6043.65	37.41	76
grandifolia	b	8	.62	19	7.42	46	11.38	7202.90	23.12	64
Fraxinus	a	155	13.33	32	12.90	50	13.51	2324.00	13.35	96
americana	b	169	13.11	82	32.03	108	26.27	2797.59	9.01	100
F.	a	—	—	—	—	—	—	—	—	—
nigra	b	—	—	—	—	1	.25	527.56	1.89	4
Gleditsia	a	—	—	—	—	—	—	—	—	—
triacanthos	b	—	—	—	—	1	.25	78.54	.25	4
Gymnocladus	a	4	.34	1	.40	3	.81	252.11	1.45	16
dioica	b	—	—	1	.39	2	.49	177.50	.58	4
Juglans	a	—	—	—	—	—	—	—	—	—
cinerea	b	1	.08	1	.39	1	.25	.78	—	8
J.	a	2	.17	—	—	—	—	—	—	4
nigra	b	—	—	—	—	1	.25	314.16	1.00	4
Lindera	a	380	32.67	21	8.46	21	5.66	18.85	.11	80
benzoin	b	665	51.59	—	—	—	—	—	—	72
Liquidambar	a	4	.34	2	.81	3	.81	563.13	3.24	20
styraciflua	b	2	.16	—	—	3	.74	807.39	2.60	12

TABLE II—(Continued)

Showing percentages of small stems, total stems, basal areas and F. I. a—north sector (25 quadrats) b—south sector (25 quadrats)

Species		Stems below 1" No.	%	Stems 1"—2" No.	%	Total stems No.	%	Basal areas sq. in.	%	F. I.
Liriodendron	a	4	.34	2	.81	13	3.51	292.95	1.70	28
tulipifera	b	1	.08	—	—	5	1.23	1135.69	3.66	24
Morus	a	15	1.29	4	1.61	4	1.08	3.14	.02	24
rubra	b	6	.47	4	1.56	5	1.23	19.63	.06	40
Ostrya	a	10	.86	8	3.22	9	2.43	15.71	.09	32
virginiana	b	1	.08	1	.39	—	.25	.78	—	8
Prunus	a	25	2.15	17	6.85	23	6.22	188.49	1.08	40
serotina	b	44	3.41	9	3.52	13	3.21	40.84	.13	40
Quercus	a	2	.17	—	—	2	.54	1614.78	9.21	16
alba	b	3	.26	—	—	3	.74	3274.33	10.54	12
Q.	a	—	—	—	—	1	.27	113.10	.65	8
bicolor	b	—	—	—	—	1	.25	2798.38	9.01	12
Q. borealis	a	2	.17	3	1.21	4	1.08	538.00	3.09	20
var. maxima	b	2	.16	1	.39	4	.99	2496.00	8.04	20
Rhus	a	202	17.37	1	.40	1	.27	.78	—	72
toxicodendron	b	42	3.26	—	—	—	—	—	—	32
Ribes	a	22	1.90	—	—	—	—	—	—	4
americanum	b	—	—	—	—	—	—	—	—	—
Rosa	a	4	.34	—	+	—	—	—	—	4
palustris	b	—	—	—	—	—	—	—	—	—
Rubus alle-	a	—	—	—	—	—	—	—	—	—
gheniensis	b	1	.08	—	—	—	—	—	—	4

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TABLE II—(Continued)

Showing percentages of small stems, total stems, basal areas and F. I. a—north sector (25 quadrats) b—south sector (25 quadrats)

Species		Stems below 1" No.	%	Stems 1"—2" No.	%	Total stems No.	%	Basal areas sq. in.	%	F. I.
R. occidentalis	a	1	.09	—	—	—	—	—	—	4
	b	—	—	—	—	—	—	—	—	—
Sambucus canadensis	a	—	—	—	—	—	—	—	—	—
	b	—	.08	—	—	—	—	—	—	4
Smilax hispida	a	9	.77	—	—	—	—	—	—	16
	b	1	.08	—	—	—	—	—	—	4
Campsis radicans	a	5	.43	—	—	—	—	—	—	4
	b	—	—	—	—	—	—	—	—	—
Tilia americana	a	7	.60	2	.81	5	1.35	762.32	4.38	24
	b	13	1.00	4	1.56	8	1.98	238.76	.78	24
Ulmus americana	a	6	.52	5	2.02	13	3.51	1602.22	9.20	40
	b	7	.54	1	.39	13	3.21	4461.07	14.31	44
U. fulva	a	19	1.63	3	1.21	3	.81	2.36	.01	24
	b	11	.86	3	1.17	5	1.23	78.54	.25	28
Viburnum prunifolium	a	19	1.63	2	.81	2	.54	1.57	.01	12
	b	17	1.32	3	1.17	3	.74	—	—	16
Vitis spp.	a	10	.86	3	1.21	3	.81	2.36	.01	28
	b	2	.16	—	—	—	—	—	—	4
Zanthoxylem americanum	a	10	.86	—	—	—	—	—	—	8
	b	4	.31	—	—	—	—	—	—	12

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AN ECOLOGICAL STUDY OF THE FLOODPLAIN FOREST ALONG THE WHITE RIVER SYSTEM OF INDIANA*

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Broad Ripple High School

As pointed out by Potzger and Friesner (9), Conard (3) and Cain (1), a mere empirical description of a forest means little as a definite presentation of conditions operating, and becomes nil in comparative studies. Most of the work on forest ecology in the United States has considered upland climax communities, and very little attention has been given the great transitional forests of the floodplains, and to the writer's knowledge only Oosting (8) has given specific quantitative data on the sociology of the species constituting the crown cover of the floodplain forests.

The present study of 20 stands was made within the White River system because it bisects not only the state from east to west but crosses four of Deam's (5) differentiated botanical areas. It was expected that forests of such a river valley would show a considerable degree of uniformity of habitat over a wide geographical area and that this would be reflected by fidelity and frequency of key species controlling the crown cover of the forest.

METHODS

Twenty stations were established. At each station twenty 100-square-meter quadrats were studied. Each of the 20 quadrats in every station was separated by a 10-meter skip.

A stout cord, subdivided into four 10-meter sections, each section having a loop, was used for delimiting each quadrat. Corner stakes were used at each loop and thus the cord could be stretched tightly, resulting in a more efficient tabulation. Wooden calipers were used to measure the DBH. of all stems one inch or over in diameter. All stems below one inch DBH. but three feet or over in height were recorded for density, frequency and fidelity. The nomenclature was that of Deam's "Flora of Indiana" (5).

Legend:
Tipton Till Plain
Illinois Drift Plain
Lower Wabash Valley
Unglaciated Area
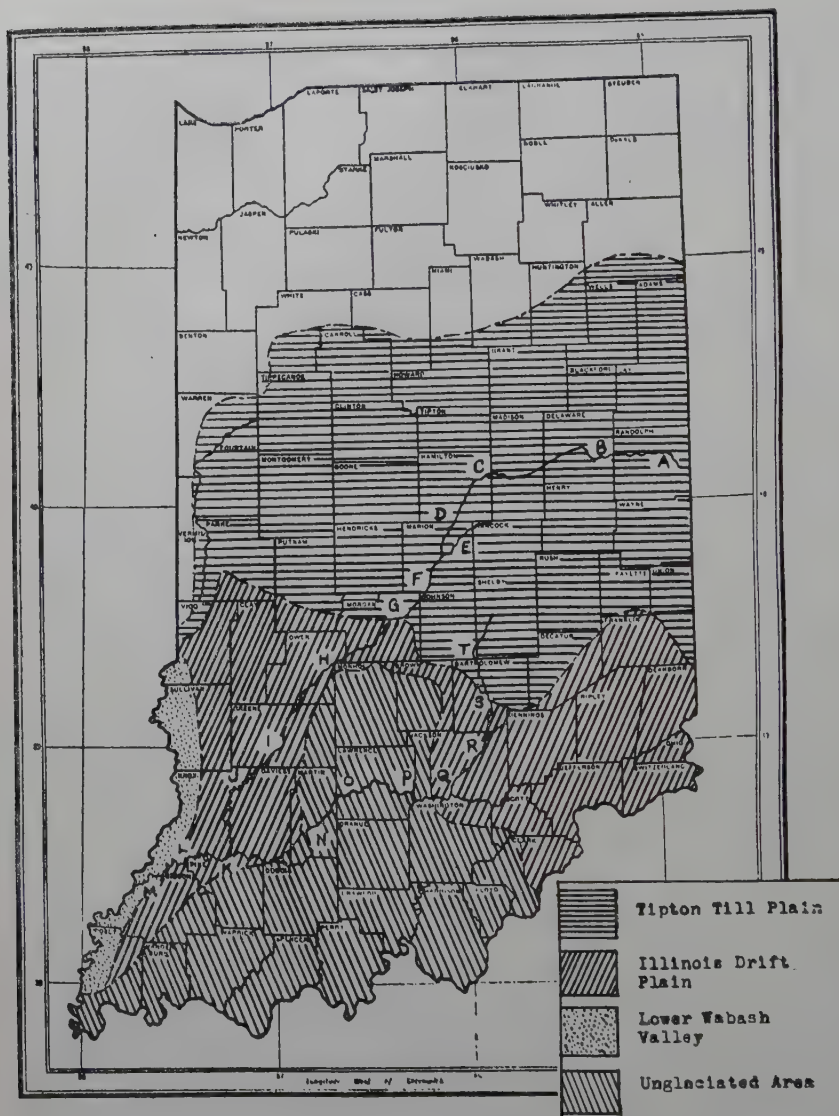
Shrubs and vines were listed and recorded only for frequency and fidelity.

LOCATION AND EXTENT OF AREA

Sample stands were located chiefly within the floodplain of the east and west forks of White River and the main river, formed by the

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junction of these two. Exceptions were one station on Fall Creek near its mouth on the west fork of White River and one station each on Sugar Creek and Driftwood River, the last two streams being the chief tributaries of the east fork.

The course of these valleys crossed the following of Deam's (5) botanical areas: the Tipton Till Plain, the Illinois Drift Plain, the Lower Wabash Valley and the Unglaciated Area. The location of the various stations in respect to Deam's botanical areas are s follows: Tipton Till Plain, Stations A-B-C-D-E-F-S-T; Illinois Drift Plain, Stations G-H-I-J-K-L-R; Lower Wabash Valley, Station M; Unglaciated Area, Stations N-O-P-Q. The 20 stations were established as nearly as possible at regular intervals. Their distribution is shown graphically in fig. 1.

LOCATION OF STATIONS

Station   Location

A   Cox farm, 6 mi. se. of Winchester, Randolph county.

B   South bank of White river, 3 mi. s. of Selma, Delaware county.

C   North bank of White river, 0.5 mi. sw. of Perkinsville, Hamilton county.

D   East bank of White river, just s. of Marion-Hamilton county line.

E   North bank of Fall creek, nw. boundary line of Fort Harrison, Marion county.

F   West bank of White river, 4 mi. nw. of Glenns Valley, Marion county.

G   East bank of White river, 0.75 mi. n. of jct. of Rds. 39 and 67, Morgan county.

H   McCormack's creek, McCormack's Creek State park, Owen county.

I.   East bank of White river, 3 mi. sw. of Bloomfield, Greene county.

J   East bank of White river, 3 mi. se. of Edwardsport, Daviess county.

K   North bank of White river, 3 mi. nw. of Petersburg, Pike county.

L   South bank of White river, 2 mi. s. of Giro, Gibson county.

M   North bank of White river, 8 mi. w. of Patoka, on Bingham farm, Gibson county.

N   East bank of the east fork of White river, 5 mi. se. of Loo-
    gootee, Martin county.
O   East bank, east fork of White river, 4.5 mi. s. of Williams,
    Lawrence county.
P   South bank, east fork of White river, 0.75 mi. n. of Rivervale,
    Lawrence county.
Q   East bank, east fork of White river, 3 mi. se. of Medora,
    Jackson county.
R   West bank, east fork of White river, 3 mi. w. of Seymour,
    Jackson county.
S   West bank of Driftwood river, 3.5 mi. nw. of Columbus,
    Bartholomew county.
T   East bank of Sugar creek, 2.5 mi. we. of Edinburg, Johnson
    county.

RESULTS AND OBSERVATIONS

Seventy-one woody species play a part in the vegetation cover for
the 20 stations. These are divided into 40 species of tall trees, 9 of
small trees, 14 of shrubs and 8 of vines. The crown cover is con-
trolled chiefly by 9 species as shown by the density, frequency and
basal area (table I). These species are *Acer negundo, A. sacchar-
inum, Celtis occidentalis, Fraxinus americana, Platanus occidentalis,
Populus deltoides, Salix nigra, Ulmus americana* and *U. thomasi*. It
is interesting to note that *Celtis occidentalis*, although high in fre-
quency and density, was low in basal area, and in the number of larger
trees as compared to *Acer saccharinum, Platanus occidentalis, Popu-
lus deltoides,* and *Ulmus americana.*

In Station "C" the predominant species was *Celtis occidentalis*
(table V). At no other station did Celtis reach the position attained
here; in fact, the status of Celtis is disjunct in its distribution, being
prominent in one quadrat and entirely lacking in an adjoining one.
Yet it attained a high fidelity for the entire study. *Acer saccharinum*
and *Ulmus americana* ranked highest in F. I. and fidelity: the former
having F. I. 50.0% and fidelity 100%; the latter having F. I. 55.75%
and fidelity 100%.

A comparison of species in the first 5 stations (table V) will show
that *Acer saccharinum* plays a very minor role as far as frequency
and abundance are concerned.

Salix nigra shows a more disjunct distribution that *Celtis occi-
dentalis.* It is entirely absent in Stations D, H, K and S (table V).

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This may at first seem surprising, but since most of these individuals are normally found colonized at the edge of the water, and since few quadrats extended to the edge of the banks, it is obvious that Salix should be lacking in some of the stations.

Populus deltoides is wanting in four stations, A, D, F and I, and is similar to Salix nigra in regard to density, frequency and fidelity (table I).

Fraxinus americana, absent in Stations E, G, I, P and Q, also shows a disjunct distribution although adding materially to the density, frequency and fidelity of the crown cover (table V).

An interesting fact of this floodplain group is the large sizes recorded for some of the individuals. A few of these with the DBH. in inches are listed as follows: *Acer saccharinum*, 38, 40, 53, 55; *A. saccharum*, 37, 47; *Populus deltoides*, 38, 39, 47; *Platanus occidentalis*, 54, 61, 66; *Quercus imbricaria*, 39, 40; and *Ulmus americana*, 37 and 38.

The second layer, i. e. small tree stratum, is weakly represented, only three species show a pronounced frequency over the others (table II). These are *Cercis canadensis* (F. I. 7.25%), *Cornus florida* (F. I. 9.25%) and *Crataegus* sp. ? (F. I. 11%). Crataegus was the outstanding small tree since it exceeded the others in density, frequency and in basal area.

In the shrub layer, *Sambucus canadensis* was the outstanding species as indicated by density and frequency (table III). However, it was surpassed in basal area by *Asimina triloba*, *Evonymus atropurpureus* and *Forestiera acuminata*. The latter had a basal area of 46.9242 square inches, a total several times greater than Sambucus. These results are to be expected since Sambucus never extended beyond the 1-inch size class.

Among the vines *Rhus radicans* was the predominant species as reflected by its frequency and fidelity (F. I. 78.5% and fidelity 100%). Its closest rival was Vitis (F. I. 48.25% and a fidelity of 100%, (table IV).

The crown cover of the floodplain forest within the Tipton Till Plain, based on frequency and abundance (table V), is as follows: *Acer saccharinum, Celtis occidentalis, Platanus occidentalis, Ulmus americana* and *U. thomasi*. Crataegus was the outstanding small tree of this area.

Only one species, *Acer saccharinum*, was found in all 7 of the stations of the Illinois Drift Plain (table V). Other species contributing

to the crown cover were: *Acer negundo, Fraxinus americana, Platanus occidentalis, Populus deltoides,* and *Ulmus americana.* Crataegus, again, was the predominent small tree of this area (table V).

The lower Wabash Valley area was represented only by Station "M" (table V). The narrowness of this area accounted for the fact that only one station was located there. The species contributing to the crown cover, as reflected by their frequency and abundance, were: *Acer saccharinum, Carya tomentosa, Celtis occidentalis, Fraxinus americana Gymnocladus dioica* and *Ulmus thomasi.* It will be noted that there were no outstanding figures for frequency and density in this station: *Acer saccharinum* having F. I. 15% and density of 31, and *Ulmus thomasi* having F. I. 40% and density of 13. It is interesting to note that *Carya tomentosa* and *Gymnocladus dioica* were not represented in the other stands. Station "M" recorded abundant representation of tall trees, but small trees were limited to one species, *Carpinus caroliniana,* var. *virginiana.*

The crown cover for the portion of the floodplain within the unglaciated area consisted of the following species: *Acer negundo, A. saccharinum, Celtis occidentalis, Populus deltoides, Salix nigra, Ulmus americana* and *U. thomasi. Prunus americana* was the predominant small tree in this area, being present in two of the four stations.

The genus Acer appeared in 307 of the total 400 quadrats for a F. I. of 76.75% and Ulmus, as a genus, appeared in 319 quadrats for a F. I. of 79.75%. Each had a fidelity of 100%. The total density of Acer, however, far exceeded that of Ulmus (table I).

DISCUSSION

Quantitative data form the only adequate basis of any ecological study. That some species of trees are characteristically limited more or less to floodplains, e. g., the willow and sycamore, is common knowledge, but the composition of a floodplain forest is more complex than the superficial impression attained by casual observances indicates. It is only by such data as presented in size-classes, density, frequency index, and fidelity that any true conception can be reached regarding the relation of plants to their environment and the real composition of a forest stand.

The east and west forks of White river and the principal river itself, today are in mature age, as evidenced by the meandering courses which they pursue, and by the wide river valley enclosed by gentle

slopes. The study of forests in such an environment may lead one to suspect a diversity of forest cover types, since the waters of these valleys pass through four of the five of the botanical areas (5) of Indiana (figure 1). That the facts are contrary to this supposition can readily be seen by comparing the frequency index and abundance of trees found in these stations (table V). As shown by tables I and V, the forest cover is primarily, and more or less uniformly, controlled by *Acer negundo, A. saccharinum, Celtis occidentalis, Fraxinus americana, Platanus occidentalis, Populus deltoides, Salix nigra, Ulmus americana* and *U. thomasi.*

The 9 principal species of the crown cover are typically colonial or gregarious in distribution as Cain (2) described the condition, for they do not form a close association as do the species constituting the climax forest (9) but rather giving rise to a mosaic pattern of "colony association."

It was, indeed, surprising that so large a number of species participate in the crown cover of a floodplain forest. Gordon (6) states that "a classification of floodplain or bottomland forest is difficult because of the large number of species involved and on account of rapid physiographic changes : such changes affect local drainage conditions, destroy old habitats and create new ones." While in the floodplain forest a larger number of species play an important part (F. I. 35% or above) in the crown cover, and the total number of species of tall trees is greater than in either the mixed mesophytic of oak-hickory types of climax forest, as recorded by Potzger and Friesner (9), the difficulty which Gordon points out is really a result of the lack of a true association of species, and the gregarious habit which determines distribution, producing, as pointed out before, a sort of "colonial association." This is plainly supported by the unusually low F. I. even for the leading species.

Acer saccharinum is the outstanding species in the lowland forest as shown by density, frequency, fidelity and basal area (table I). *Ulmus americana* has a greater F. I. than *Acer saccharinum* (*Ulmus americana* 55.75% and *Acer saccharinum* 50.0%), however, it is surpassed by the latter in density and basal area.

The leading and most characteristic genera in the floodplain forest are Acer and Ulmus. A comparison of these genera with respect to F. I. and fidelity shows that there is little difference in importance between the two (table I), and even for these genera the F. I. seems rather low (Acer F. I. 76.76% and Ulmus 79.75%) when compared

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with the F. I. of the leading genera in upland forest of the same regions. Potzger and Friesner (9) show that on southeast slopes in central Indiana *Acer saccharum, Carya glabra,* and *Quercus montana* attain a frequency index of 100%. This apparently is further proof of a gregarious habit even for the genera which primarily control the crown cover in floodplain forests.

The mortality among the young of Celtis is evidently very high as shown by the large number of stems below one inch DBH. and the relatively small number of trees that are above one inch DBH. (table I). Potzger and Friesner (10) found that a similar condition existed with *Fraxinus americana* in their comparison between virgin forest and adjacent areas of secondary succession. Weaver and Clements (12) state that "in the case of woody plants, seedlings are notably tolerant of shade when contrasted with their demands in later life." Apparently Celtis reproduces well but suffers high mortality beyond the seedling stage.

The remaining eight members most commonly participating in the crown cover as listed earlier in this discussion show good reproduction as evidenced by the large number of stems above one inch DBH. in comparison with the totals for the seedling stage (table I). It is interesting to note that *Fraxinus americana* is included among those members of the floodplain forest type capable of good reproduction.

Cowles (4) shows that *Salix nigra, Acer saccharinum, Populus deltoides* and *Fraxinus americana* are important in the establishment of a floodplain forest because they are the first to appear. "The willows are found on the margin and the river maple (*Acer saccharinum*), the cottonwood (*Populus deltoides*), and the ash (*Fraxinus americana*) soon come in." This analysis agrees well with the present study. Oosting (8) found that the earliest woody community on floodplains and islands is invariably a willow-alder thicket and if the habitat remains poorly drained other hardwoods may not appear in significant numbers for a much longer time than on better drained sites. Since no attempt at zonation was made in this study, some stations being established farther back from the river and on higher banks than other sites, and since both conditions eliminate to some extent disturbances caused by flooding, the absence of Acer, Fraxinus, Populus and Salix in a few of the stations (table V) is only natural. The remaining members adding to the cover show a better representation throughout the entire floodplain.

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The distribution of all the species just discussed emphasize the modified association of species which can perhaps be attributed to the influence of light. All of the species are very likely more or less intolerant, and all produce abundant seeds which germinate well. Reproduction is thus limited to open spaces after windfall or death of old trees, and the species which chance to be nearest such an unoccupied space will establish a colony. Soil moisture is not a limiting factor for the species involved in floodplain forest. A floodplain forest, thus, is somewhat similar to the rainforest where dominance is absent or poorly defined (12).

The small tree and shrub layers were poorly expressed. Crataegus, typical of early secondary succession, was the predominant small tree (table II). *Sambucus canadensis,* also an invader of secondary succession, was outstanding for the shrub layer (table II). Both Crataegus and Sambucus were found only in more or less open regions. This would indicate their intolerance of shade. Potzger, Friesner and Keller (11) found that in a mature stand of forest primeval, a well-developed small-tree under-story is lacking and that the shrub layer is represented chiefly by one species, *Asimina tribola.* Thus it can be said that the position of small trees and shrubs in a floodplain forest is similar to that found in some mature upland stands.

A list of the forest climax by botanical areas will show the following: for the Tipton Till Plain, beech-maple is the principal climax (6). The Illinois Drift Plain has two principal climaxes as shown by Potzger and Friesner (9), i. e., a beech-maple climax on north-facing slopes and an oak-hickory climax on the south-facing slopes; the unglaciated area consists chiefly of beech and beech-maple stands and mixed forest areas with oak-hickory on the uplands, beech-sugar maple, and beech-sugar maple-yellow poplar sub-types as segregates of the mixed mesophytic forest, as determined by Gordon (7); the Lower Wabash Valley area has the nearest approach to the floodplain forest, the association being elm-ash-maple and may include sweet gum, pin oak and a wide variety of other mixed hardwoods. The Wabash Valley area is, of course, a floodplain with variation in maturity because of greater width.

The floodplain is apparently a very uniform habitat where macroclimate more definitely determines the establishment of tree species, and where modifying effect of microclimate is reduced to a minimum. The established floodplain, the habitat considered in this study, is controlled by forest which is the immediate predecessor to the climax

mesophytic forest, where soil moisture conditions are less rigorous than in the uplands and the habitat is quite uniform over wide geographical areas, not influenced by heterogeneous upland sites which border on the river valley.

SUMMARY AND CONCLUSIONS

1. The paper presents an ecological study of the floodplain forest within the White River system. It is based on four hundred 100-square-meter quadrat tabulations.

2. Forty species of tall trees take part in the crown cover, nine species in the small tree stratum, and fourteen species in the shrub layer.

3. The outstanding species in the crown cover are *Acer negundo*, *A. saccharinum, Celtis occidentalis, Fraxinus americana, Platanus occidentalis, Populus deltoides, Salix nigra, Ulmus americana* and *U. thomasi.*

4. *Acer saccharinum* and *Ulmus americana* ranked highest in fidelity, each having 100%. *U. americana* had the highest frequency index with 55.75%.

5. A well developed small tree and shrub layer is lacking. The most common small tree is Crataegus with F. I. 11.0%. The outstanding shrub is *Sambucus canadensis* with F. I. 37.0%.

6. Celtis is the only member in the principal crown cover that has a high rate of mortality among the seedlings.

7. There is no decided difference in the floodplain forest within a river system which bisects four of Deam's botanical areas encountered in this investigation.

8. While fidelity is high for 9 species of tall trees commonly important in the crown cover, the association is poorly expressed. This is due to gregarious or colonial habits which influence or determine the distribution of the species within the stand.

9. Macroclimate apparently is more of a determining factor for the establishment of tree species in the floodplain than is macroclimate.

10. The outstanding features shown by the study: (a) the large number of tall tree species participating in control of the crown, (b) the gregarious or colonial habit of the most prominent species in the stands, making for a poorly expressed association, (c) the simi-

larity of the numerous stands throughout the river system which passes through a number of botanical areas marked by striking differences in the association complex of the upland forest.

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TABLE I

Tall trees in size classes, showing Frequency Index, Fidelity and Basal Area.

Species	Below 1 in.	1 in.	2-5	6-10	11-15	16-20	Above 20	Total Stems	F. I.	Fidelity	Basal Area Sq. Ft.
Acer negundo	689	54	118	62	15	11	2	951	46.25	90.0	63.620
A. rubrum	335	22	59	11	3			477	15.00	40.0	33.960
A. saccharinum	735	92	341	301	136	63	30	1698	50.00	100.0	486.542
A. saccharum	4					1		5	.50	5.0	2.180
Aesculus glabra	32	5	16	17	4	1	2	77	7.75	35.0	17.700
Ailanthus altissima	2		2	2				6	1.25	10.0	7.745
Carya cordiformis	9		1			1	2	13	1.00	15.0	7.467
C. illinoensis				2	1			3	1.00	5.0	1.816
C. laciniosa	12			1	2			15	1.25	10.0	2.493
C. tomentosa			1	2				3	1.00	5.00	.567
Catalpa speciosa	2		1					3	.50	5.0	.049
Celtis occidentalis	1688	133	158	99	23	22	9	2132	39.24	95.0	138.306
Fagus grandifolia			1			1	1	3	.25	5.00	4.918
Fraxinus americana	451	47	49	47	15	17	3	629	34.75	85.0	92.740
F. lanceolata	28	1	2	4				35	5.50	40.0	1.965
F. nigra	20			4			2	26	1.25	20.0	6.944
F. pennsylvanica						2		2	.50	5.0	3.736
F. quadrangulata	3		1	1	2			7	1.50	20.0	2.209
F. tomentosa	2	2	4					8	1.75	20.0	.190
Gleditsia aquatica	15		3		1			19	.75	10.0	1.619
G. triacanthos	139	7	17	20	13	14	4	214	17.75	75.0	55.14
Gymnocladus dioica	5	2	6		2			15	1.00	5.0	2.601
Juglans cinerea			4	5				9	1.50	15.0	1.843
J. nigra	29	4	12	8	13	5		71	12.50	90.0	23.753

TABLE I (Continued)

Tall trees in size classes, showing Frequency Index, Fidelity and Basal Area.

Species	Below 1 in.	1 in.	2-5	6-10	11-15	16-20	Above 20	Total Stems	F. I.	Fidelity	Basal Area Sq. Ft.
Liquidambar styraciflua	32	1	2	7	3			45	1.00	20.0	5.508
Morus rubra	78	6	6	5		1		96	10.25	75.0	5.479
Nyssa sylvatica	6		1					7	.75	10.0	.218
Platanus occidentalis	90	14	52	67	89	58	94	464	37.00	95.0	643.633
Populus deltoides	10	1	14	36	54	69	68	252	27.50	80.0	376.357
Prunus serotina	36	5	2	1				44	1.75	10.0	.218
Quercus bicolor	11	2	2	2			3	20	3.50	20.0	20.828
Q. imbricaria	3	3	2	3	1			12	.75	15.0	2.383
Q. montana	1		1		1			3	.75	10.0	1.058
Q. muhlenbergii	5	3					1	9	.50	5.0	4.734
Q. stellata			1	1				2	.50	10.0	.218
Salix nigra	96	7	19	60	32	5	3	222	44.75	85.0	70.549
Tilia americana	21	2	10	7	6	2	3	51	4.00	45.0	24.587
Ulmus americana	188	37	150	137	78	24	28	642	55.75	100.0	246.945
U. fulva	88	9	26	24	6	1	2	156	20.75	67.0	20.736
U. thomasi	35	18	166	117	36	6	4	382	33.25	80.0	90.995

TABLE II

Small trees in size classes showing Frequency Index, Fidelity and Basal Area.

Species	Below 1 in.	1 in.	2-5	6-10	Total Stems	F. I.	Fidelity	Basal Area Sq. In.
Carpinus caroliniana var. virginiana	10	11	3		24	1.75	15.0	18.0642
Cercis canadensis	64	11	18	3	96	7.25	40.0	308.1622
Cornus florida	323	23	7		353	9.25	50.0	66.0536
Crataegus	306	75	114		510	11.00	45.0	1571.5856
Maclura pomifera			3		3	.50	5.0	17.2788
Ostrya virginiana	26	22	27		75	1.00	20.0	205.7748
Prunus americana	89	10	16	2	117	.75	5.0	253.2420
P. hortulana	5	3	1		9	1.25	5.0	9.4248
Salix discolor	5	2	3		10	.50	10.0	31.4160

TABLE III

Shrubs in size classes, showing Frequency Index and Fidelity

Species	Below 1 in.	1 in.	2-5	Total Stems	F. I.	Fidelity
Amorpha fruticosa					1.0	5.0
Asimina triloba	45	2	4	51	3.0	25.0
Evonymus atropurpureus	144	10	2	156	7.5	35.0
Forestiera acuminata	112	19	6	137	.75	5.0
Gaylussacia baccata					5.5	15.0
Grossularia cynosbati					.75	10.0
Lindera benzoin	173	7	2	182	6.0	40.0
Prunus virginiana	13			13	1.0	5.0
Ptelea trifoliata	144	3	2	149	3.5	40.0
Rosa sp. ?					5.25	10.0
Rubus sp. ?					3.0	20.0
Sambucus canadensis	1537	16		1553	37.0	68.0
Staphylea trifolia	3			3	.75	10.0
Viburnum lentago					.75	15.0

TABLE IV

Showing Frequency Index and Fidelity of Vines

Species	F. I.	Fidelity
Aristolochia tomentosa	1.0	5.0
Bignonia capreolata	1.75	15.0
Campsis radicans	25.5	55.0
Celastrus scandens	.75	10.0
Parthenocissus quinquefolia	15.5	60.0
Rhus radicans	78.5	100.0
Smilax	39.5	95.0
Vitis	48.25	100.0

TABLE V

Frequency Index and Density of Species by Stations.

Species	A F. I.	A Density	B F. I.	B Density	C F. I.	C Density	D F. I.	D Density	E F. I.	E Density
Acer negundo	5.0		45.0	21	25.0	8	65.0	29	95.0	45
A. saccharinum		1	20.0	7	10.0	5	45.0	23	95.0	38
A. saccharum							5.0	1		
Aesculus glabra	5.0	1	5.0	1			15.0	6	15.0	6
Carya cordiformis	15.0	3			5.0	2				
Celtis occidentalis	10.0	2	15.0	6	100.0	102	80.0	47	40.0	29
Cercis canadensis							10.0	2	10.0	2
Crataegus sp. ?	85.0	156			25.0	13	5.0	2		
Fagus grandifolia	10.0	2								
Fraxinus americana	25.0	8	60.0	27	15.0	6	15.0	6	10.0	3
F. lanceolata			5.0	6			5.0	1		
F. nigra	10.0	2								
F. pennsylvanica	10.0	4								
F. quadrangulata	5.0	1			5.0	1	5.0	1		
F. tomentosa			15.0	3						
Gleditsia aquatica			20.0	5						
G. triacanthos	45.0	12			10.0	6	15.0	3	5.0	1
Juglans cinerea									10.0	2
J. nigra	5.0	1	15.0	3			5.0	1		
Ostrya virginiana									10.0	3
Platanus occidentalis	15.0	7	45.0	31	55.0	25	25.0	11	50.0	21
Populus deltoides			25.00	12	10.0	2			45.0	12
Prunus americana	20.0	7								
Quercus bicolor	50.0	5							25.0	9

TABLE V (Continued)

Frequency Index and Density of Species by Stations.

Species	F. I. (A)	Density (A)	F. I. (B)	Density (B)	F. I. (C)	Density (C)	F. I. (D)	Density (D)	F. I. (E)	Density (E)
Q. imbricaria					5.0	1				
Q. montana	5.0	1								
Q. stellata			5.0	1						
Salix discolor					10.0	4				
S. nigra	15.0	9	25.0	14	35.0	15			25.0	6
Ulmus americana	30.0	7	45.0	13	85.0	56	50.0	14	70.0	53
U. fulva	30.0	12	30.0	6	40.0	12	85.0	9		
U. thomasi	15.0	4	75.0	23	60.0	28	25.0	8	80.0	35

Species	F. I. (F)	Density (F)	F. I. (G)	Density (G)	F. I. (H)	Density (H)	F. I. (I)	Density (I)	F. I. (J)	Density (J)
Acer negundo	40.0	19	40.0	23	35.0	26	15.0	6	25.0	14
A. rubrum			35.0	18			5.0	2	30.0	9
A. saccharinum	40.0	22	75.0	67	15.0	18	80.0	103	35.0	24
Aesculus glabra	5.0	1								
Catalpa speciosa									10.0	3
Celtis occidentalis	65.0	50	5.0	2	5.0	2	65.0	43	60.0	34
Cercis canadensis			5.0	2						
Cornus florida					5.0	2	10.0	4		
Crataegus sp. ?	10.0	6					10.0	11	10.0	4
Fraxinus americana	25.0	13			15.0	14	10.0		10.0	3
F. lanceolata	5.0	1								
F. tomentosa					5.0	3				
Gleditsia triacanthos	25.0	9					30.0	18		

TABLE V (Continued)

Frequency Index and Density of Species by Stations.

Species	F F.I.	F Density	G F.I.	G Density	H F.I.	H Density	I F.I.	I Density	J F.I.	J Density
Juglans nigra	10.0	2					5.0	4		
Morus rubra			5.0	3					10.0	3
Platanus occidentalis	15.0	3	5.0	1	65.0	62	55.0	20	50.0	19
Populus deltoides			65.0	58	10.0	3			50.0	26
Quercus bicolor									5.0	1
Salix discolor							5.0	1		
S. nigra	10.0	2	5.0	2			15.0	4		
Tilia americana	5.0	1	5.0	1			15.0	5		
Ulmus americana	65.0	19	30.0	9	10.0	2	50.0	35	40.0	4
U. fulva	10.0	3	15.0	5	20.0	5	10.0	3		
U. thomasi	20.0	6	40.0	16	30.0	17	30.0	12	50.0	20

Species	K F.I.	K Density	L F.I.	L Density	M F.I.	M Density	N F.I.	N Density	O F.I.	O Density
Acer negundo	20.0	12			5.0	2	60.0	22	10.0	3
A. rubrum	20.0	15	65.0	106	15.0	4			5.0	4
A. saccharinum	45.0	29	50.0	64	15.0	31	25.0	13	90.0	103
A. saccharum					10.0	2				
Aesculus glabra							70.0	30		
Carpinus caroliniana var. virginiana					5.0	1				
Carya illinoensis					30.0	18				
C. laciniosa	5.0	1			5.0	1				
Celtis occidentalis	35.0	14			20.0	12	40.0	21	50.0	22
Cercis canadensis	5.0	1					10.0	5		

TABLE V (Continued)

Frequency Index and Density of Species by Stations.

Species	K F. I.	K Density	L F. I.	L Density	M F. I.	M Density	N F. I.	N Density	O F. I.	O Density
Cornus florida	10.0	2			5.0	1	15.0	4		
Crataegus sp. ?	30.0	15								
Fagus grandifolia	5.0	1								
Fraxinus americana	5.0	1	45.0	33	35.0	13	30.0	24	55.0	42
F. lanceolata					10.0	2	5.0	1		
F. nigra					5.0	5	10.0	3		
F. quadrangulata			5.0	3						
Gleditsia triacanthos	25.0	14	5.0	1	5.0	1			15.0	9
Gymnocladus dioica					15.0	10				
Juglans cinerea									10.0	4
J. nigra	10.0	2			10.0	2	40.0	11	25.0	8
Liquidambar styraciflua			5.0	1	15.0	7			5.0	2
Morus rubra	5.0	1					10.0	3		
Nyssa sylvatica			10.0	2			5.00	1		
Ostrya virginiana	10.0	3					50.0	34		
Platanus occidentalis	80.0	42			20.0	5	30.0	16	80.0	29
Populus deltoides	25.0	10	60.0	27	15.0	6	10.0	6	30.0	11
Prunus hortulana			30.0	26			5.0	1		
Quercus bicolor	5.0	1								
Q. imbricaria	20.0	6								
Salix nigra	5.0		25.0	15	10.0	7	10.0	4	40.0	10
Tilia americana	5.0	1			5.0	1	10.0	2	10.0	2
Ulmus americana	45.0	21			30.0	6	60.0	23	80.0	39
U. fulva	5.0	13			10.0	2			10.0	2
U. thomasi	60.0	45			40.0	13	40.0	17	35.0	16

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TABLE V (Continued)

Frequency Index and Density of Species by Stations.

Species	P F. I.	P Density	Q F. I.	Q Density	R F. I.	R Density	S F. I.	S Density	T F. I.	T Density
Acer negundo	5.0	3	30.0	9	40.0	14	35.0	16	50.0	29
A. rubrum	20.0	104	20.0	19	85.0	80			50.0	73
A. saccharinum	60.0	65	50.0	46	50.0	31	85.0	89	5.0	2
Aesculus glabra									35.0	16
Celtis occidentalis	15.0	6	55.0	42	20.0	8	20.0	6	20.0	6
Cercis canadensis									25.0	10
Cornus florida										
Crataegus sp. ?			5.0	5						
Fraxinus americana	65.0	48	15.0	6	5.0	1	30.0	7	60.0	36
F. lanceolata					5.0	1			10.0	2
F. pennsylvanica										
F. quadrangulata							5.0	1	20.0	6
F. tomentosa							5.0	1		
Gleditsia triacanthos			10.0	3	5.0	2	5.0	1		
Juglans nigra	10.0	4	10.0	2	5.0	1			10.0	3
Liquidambar styraciflua	5.0	3								
Maclura pomifera	10.0	3							5.0	3
Morus rubra			5.0	1	10.0	3				
Platanus occidentalis	75.0	42	5.0	1			30.0	6	35.0	28
Populus deltoides	5.0	1	30.0	10	55.0	34	20.0	6	5.0	4
Prunus americana	5.0	1	65.0	33						
Quercus imbricaria									10.0	6
Q. muhlenbergii										
Q. stellata			5.0	1					5.0	3

TABLE V (Continued)

Frequency Index and Density of Species by Stations.

Species	F. I.	P Dessity	F. I.	Q Dessity	F. I.	R Dessity	F. I.	S Dessity	F. I.	T Density
Salix nigra	60.0	29	20.0	4	15.0	9			5.0	1
Tilia americana	20.0	9								
Ulmus americana	80.0	29	70.0	34	60.0	37	55.0	21	90.0	59
U. fulva			30.0	9	45.0	21	20.0	4	5.0	1
U. thomasi	40.0	23	25.0	16	35.0	12	35.0	8	60.0	19

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A PRELIMINARY STUDY OF SACHERIA IN WESTERN NORTH AMERICA[1]

By C. Mervin Palmer

Lemanea from both Europe and America is being studied to determine whether the representatives from the two continents are distinct, and whether there are undescribed species to be recognized particularly for American forms. The two subgenera, Eulemanea and Sacheria, are found on both continents (4). Occasionally plants of both the subgenera have been collected growing close together in the same stream (5, 6), but there are no indications that hybridization takes place. Several hundred specimens of Lemanea have been studied by the writer and in no case have any plants been discovered which could be considered as intermediate between Eulemanea and Sacheria.

Sirodot (7) recognized Sacheria as a separate genus but Ketel and later Atkinson (1) reduced it to a subgenus of Lemanea, and most phycologists have followed the latter procedure up to the present time. Atkinson's reason for combining Sacheria and Eulemanea into one genus was that "While the structural characters of the plants clearly show a natural division, the reproductive organs present only minor variations. The structural differences alone do not seem of sufficient value to warrant the acceptance of more than one genus." However, since there appears to be no hybridization and no occurrence of intermediates between Sacheria and Eulemanea, and since the distinctions do include differences in the location of the antheridia, procarps and carpospores, in addition to the difference in construction of the sexual strands, the present writer considers that it will be justifiable and desirable to follow Sirodot in raising Sacheria Sirodot to the rank of genus and retaining the forms now in the subgenus Eulemanea in the genus Lemanea Bory emend. Sirodet. Even in very young or very old material, the two groups can be distinguished by crushing a portion of the sexual strand and determining whether the central filament is naked or closely surrounded by a number of other filaments. The former arrangement is found in Sacheria and the latter in Eulemanea.

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[1] A contribution in recognition of the 25th Anniversary of the Botany Department of Butler University.

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The described species of the two genera are generally unsatisfactory for identification of American material. Atkinson, after having studied numerous specimens from many places in North America, found so many variations and species intermediates that he finally combined several European species of Sacheria and placed almost all of the American material of that genus into the unwieldy and variable species aggregate, *Lemanea* (*Sacheria*) *fucina* (Bory) Atkinson. He indicated as his only other alternative that "one could make a species for specimens from nearly each different locality."

When he considered the other genus, Lemanea, however, he refused to combine all of the American material into one large variable species. In fact, he actually added three new species to the list. This was done in spite of the fact that many forms from Virginia, Indiana, California, Kentucky and the southeastern states did not fit well any of the described species, either new or old. A specimen from Virginia was first listed by him as *L. nodosa* and later he changed it to *L. torulosa*. Material from Indiana was first identified by him as *L. catenata*, but upon re-examination, he decided to change it to *L. annulata*. From California he described a new variety intermediate in characteristics between two recognized species. In the southeastern states, he placed all of the variable specimens into one of his new species primarily because of similar geographic location. It appears that European phycologists have paid very little attention to American specimens of Lemanea since Atkinson's articles (1, 3), but, for their own continent, they have, as a rule, continued to recognize as separate species those which Atkinson combined into one for the American material.

A restudy of the species and varieties as recognized by Sirodot indicates that one might well consider his work as a basis for the classification of these algae rather than placing too much emphasis upon that of Atkinson. The differences between species which he recognized are, in general, clear and distinct, and some of these differences were apparently not given much final consideration by Atkinson. It is true that American material does not fit the descriptions of European species, but it appears to make for more confusion to try to alter European descriptions to fit American forms.

Skuja (8) states that for Lemanea (including Sacheria), "Its center of development —— is to be found to all appearances on the North American continent." In line with this, an intensive study of the American material has forced the present writer to assume that

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there are probably a number of American species, more or less well defined, which are distinct from the European species.

Considering now the American material of Sacheria, we note that there have been no new species recognized for this continent. Atkinson (2) listed one in 1904, only to recall it a few years later. His suggested species, however, with slight modifications could readily represent a common American type. The best characteristic to separate the European from the American forms of Sacheria is the location of the carpospores in the sexual strands. All of the European forms appear to have the spores and the procarps located in both the nodal and the internodal zones with about equal distribution in both zones, while American material either has the spores and procarps limited to the nodal regions, or if they extend all or part way into the internodal regions, they are more concentrated in the nodes than in the internodes. There are very few exceptions to this arrangement and even the exceptions may be a misinterpretation due to displacement of loose, mature spores.

Geographically, the North American forms of Sacheria can be divided rather readily into three groups, the northeastern, the southeastern and the western. Most of the specimens with much-branched sexual strands are from the northeast, only one collection from the west showing this character. The great majority of sexual strands with an undulate surface are from the west, those of the two eastern groups being generally cylindric with abrupt nodes even when containing mature spores. Most of the southeastern forms are green in color while various colors such as brown, green, violet and black-violet are found elsewhere. Strands with rough, gnarled nodes are not found in the west although they are fairly common in the east. Capillary forms are not encountered in the southeastern area but are present in the western and northeastern regions.

One is led to assume, from such a study, that each American species is likely to be confined to a limited geographic area. One of the best examples of this is to be found in specimens collected in Colorado and Utah. These small, capillary, brown-violet forms with spores in both nodes and internodes of the cylindric strands, with only slightly protruding antheridial papillae, and with attenuate rather than abruptly stipitate bases are distinct from specimens found in other parts of the continent. Another group of specimens, principally from Massachusetts and Ontario is characterized by small, brown, generally unbranched strands with abruptly raised, somewhat gnarled nodes,

and with 3-7 large flat-topped, frequently confluent papillae at each node. The base is an abrupt, long cylindric stipe.

It is possible, therefore, that with continued study of even more specimens, a dozen or more American species of Sacheria eventually may be recognized. It does not appear that any of these will correspond to those described for Europe. As Atkinson (1) has indicated, the American forms resemble *S. rigida* and *S. fucina* more closely than they do *L. fluviatilis*. Since the writer has found no European specimen which has carpospores limited to the nodes, he sees no basis for that characteristic being used to distinguish between *S. fluviatilis* and the other two species mentioned above as has been claimed by Atkinson. Rather it appears to be a distinction between all European forms on one hand and the American forms on the other.

Plants of the genus Sacheria in western North America have been found in Arizona, California, Colorado, Montana, Oregon, Utah, Washington and British Columbia. Most of the collections, so far, are from California. It would seem that there may be at least five or six species of Sacheria to be recognized in this area. The plants from Colorado and Utah which have been described above constitute one group. A second group is one to which quite a number of plants from the other western states belong. The sexual strands of this second group are distinctly undulate with no tendency during the spore-forming stage from April to September to be cylindric. The strands have a short, frequently abrupt stipe which is up to 5 mm long, 2-3 indistinct antheridial papillae per node, and carpospores which are in the nodes and may extend to all but the very center of the internodes. The strands are flexible rather than rigid and when mature vary from 2-17 cm in length. About half of the specimens have a medium brown color while the others vary from green to violet or black-violet. It is quite possible that the vividly colored ones may represent a group separate from the brown ones. This cannot be determined until more specimens have been studied. Plants in this second group are from Arizona, California, Montana, Oregon and Washington. The Sacheria reported from British Columbia (9) has not yet been seen by the writer.

In the third western type of Sacheria, the sexual strands are "thick, rigid, horny," corresponding to Sirodot's European *S. rigida* in this respect. All of the western representatives are from California. Most of them are dwarf forms, being only 1-2 cm long when mature, although an occasional strand may be as much as 8 cm long.

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When young the strands may be violet but they soon change in maturing to become a characteristic yellow to yellow-brown. They have a rather plane surface with 2-3 slightly raised papillae per node. The base tends to be short and thick and not abruptly stipitate. The peripheral cell layer is generally 90-100 microns thick and 4-5 cells thick rather than 3 cells thick as in most Sacherias. The "thick, rigid, horny" characteristic can easily be recognized when the strands are observed dry under the low magnification of a binocular dissecting microscope. The Chantransial filaments of this form appear to remain even through June and July and to form a dense hemispherical mass.

The fourth western type of Sacheria is a capillary, dwarf form resembling the second type in its undulate form of the strand and the brown to brown-green color. The mature strands range from 0.7-3.5 cm in length and their maximum node diameter is only 0.5 mm. Plants of this group have been collected in California and Montana.

The fifth and final group is represented, so far, by only one collection and it is from California. The sexual strands are distinctly cylindric rather than undulate even though abundant spores are present. They are dark brown to black-violet in color and extend up to 8.5 cm in length. The papillae, 2-5 per node, are somewhat raised and are frequently confluent when old. The form is flexible rather than rigid and is not capillary. Spores are limited to the nodes. The base of each strand is an abrupt stipe, 8-13 mm in length, and branching of the strand is fairly common at the top of the stipe.

After it has been possible to group the eastern American forms, it is planned to compare these with the western groups and the European species with the possibility of definitely recognizing and describing the American species of Sacheria. The writer hopes to be able to carry this out in the near future.

Specimens of Lemanea and Sacheria from herbaria of the Chicago Natural History Museum and the University of California, in addition to smaller numbers from other sources, have been made available for this study and the writer expresses his appreciation to those in charge of the herbaria who have made the study possible.

SUMMARY

It is planned to follow Sirodot in the recognition of Sacheria as a genus rather than as a subgenus under Lemanea. Lack of hybridization between the two genera is emphasized.

American material of both Lemanea and Sacheria appears to belong to species which are distinct from those of Europe. Only a few American species have, as yet, been described.

North American material of Sacheria can be divided into three groups, the northeastern, southeastern and western, with certain distinctive characteristics recognized for each.

Western American plants of Sacheria appear to fall into five specific groups, the cylindric, small-noded, the large, undulate, the thick, rigid, horny, the dwarf undulate, and the cylindric, distinctly noded forms. These groups are not yet recognized as species pending further study of both eastern and western specimens of Sacheria.

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THE PINE BARRENS OF NEW JERSEY, A REFUGIUM DURING PLEISTOCENE TIMES*

By J. E. POTZGER

In 1943 Potzger and Otto (13) published the first paper on the pollen analyses of New Jersey peat which involved a series of five bogs from northern and northwestern New Jersey. These bogs represented a rather large geographical area, but their message was unusually uniform. One might, therefore, be justified to assume that the study gave a rather trustworthy history of the vegetation of the glaciated part of the state. From a forest constituted almost entirely of Abies, Picea, and Pinus, succession carried dominance to a pronounced Pinus period. This genus contributed as much as 80% of the pollens at these particular foot-levels. In the upper third of the sediment an association of Tsuga and Quercus depressed Pinus considerably; and in the topmost levels Castanea entered as last invader of the crown cover.

A second series of peat samples was taken within the unglaciated section of central and southern New Jersey, known as the Pine Barrens. Analysis of peat from the eight bogs forms the basis of this paper (fig. 2). Results showed so striking a difference in the history of the vegetation here as compared with that of the glaciated part of New Jersey that one was almost taken by surprise. The outstanding features of the record are a weakly expressed succession, and a heterogeneous composition of the forest, which was uniformly the same for the time during which the peat accumulated.

GEOLOGY AND PHYSIOGRAPHY

The Pine Barrens region soils are more ancient than those of northern New Jersey, dating the origin, in part at least, to Tertiary times. In 1898 Salisbury (14) postulated the theory that during Miocene times the southern part of New Jersey subsided, and eroded materials were deposited over it, giving rise to what is known as Beacon Hill. This remained elevated above sea level during subsequent submergence of the lower coastal areas. In a more recent report of
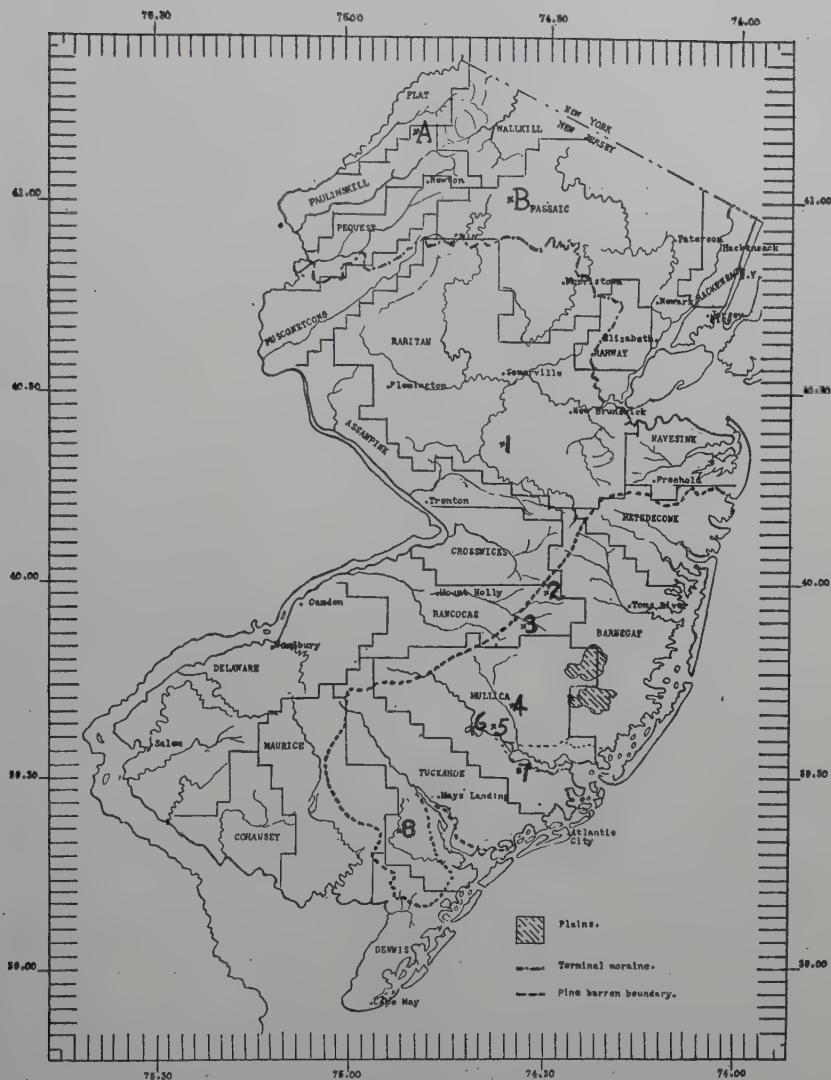

Figure 1. Map of New Jersey showing approximate location of bogs: A. Culvers Lake Bog. B. Upper Longwood Valley Bog. 1. Monmouth Junction. 2. Whiting. 3. Long Causeway. 4. Martha. 5. Bulltown. 6. Mullico River. 7. Port Republic. 8. Hunters Mills. (Map from Waksman [20]).

1902, Salisbury (15) postulates a subsidence of the land during a part of the glacial period which would have resulted in a great sound across the state from Raritan bays on the northeast to the Delaware at Trenton. South of this sound were some islands.

According to Lutz (12), Salisbury and Knapp in 1917 questioned the earlier Beacon Hill island theory by saying, "It is not known how high the land stood relative to sea level in the (Pensauken) epoch."

In the present study we are not concerned with the controversy relative to the Pine Barrens and its characteristic vegetation but only with the southern half of the state as a land mass during Pleistocene times. And both reports solve our problems satisfactorily by assuming at least some exposed land surfaces in the Beacon Hill area.

In the northern third of the state the Wisconsin ice sheet not only obliterated physiographic features by deposition of till, but also annihilated the existing vegetation. The drainage disturbances gave rise to lakes and subsequently to numerous bogs.

The writer agrees fully with Lutz (12) and Fernald (5) that it hardly requires an involved theory to explain the migration of plants to unoccupied areas. The law which controls such phenomena is no doubt as old as the plant kingdom. It involves centers of distribution and unoccupied suitable habitats, involving both climatic and edaphic factors. Since the southern part of New Jersey was above water level, either as one large island or as several islands, it could have become a haven of retreat for plants hard pressed by invading ice masses in the north.

THE PRESENT VEGETATION

In determination of the present vegetation we have consulted the publications by Stone (16), Britton (2), Taylor (17), and Hollick (11). Taylor suggests that "at the advance of the ice there must have been a great invasion of northern species, many of which are still found in the Pine Barrens." He differs with Hollick (11) by saying that Tsuga is today unknown in the Pine Barrens.

In an analysis of the type which forms the basis of this paper, we are, of course, concerned especially with pollens of the trees, which would also draw attention to the present forest cover. Stone (16) describes this as follows, "There are woods of rather tall pine with practically no oaks of any size but with an undergrowth of scrub oak and huckleberries. Then there is a more open growth in which oaks, mainly *Quercus marylandica*, reach a fair size. Other sections are

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covered with a dense growth of oaks including *Quercus marylandica,
Q. illicifolia, Q. alba, Q. velutina.* It seems to me that the first two
types are the natural and primitive ones while the solid oak growth
covers recent clearings." He considers *Pinus rigida* the pine of the
barrens, but adds that *P. echinata* is common. He continues, "Next
to *P. rigida Chamaecyperis thyoides* is the most characteristic tree of
the Barrens. Castanea is now rare, *Betula populifolia, Ilex verticillata*
are common, while *Ilex laevigata* and *I. glabra* are common in moist
ground." Taylor (17) states that Liquidambar and Nyssa are com-
mon in the woods in southern counties.

THE BOGS STUDIED

The brief descriptions were taken from the field notes of the
men who collected the peat.

MONMOUTH JUNCTION BOG. This is the northernmost one, lo-
cated in Stone's (16) Middle District. The field notes state it is
located in the Coastal Plain, at the edge of the Piedmont Plain. A
peat deposit of four feet rests on hardpan.

WHITING CEDAR SWAMP. Four feet of forest peat rest on sand.

LONG CAUSEWAY CEDAR SWAMP. The well-decomposed, slightly
woody, peat includes some charcoal to the two-foot level. The sub-
soil is sand.

CEDAR SWAMP AT MARTHA. The sampling was made in the in-
terior of this extensive swamp. Depth of peat is five feet, which is
underlain by sand.

CEDAR SWAMP AT BULLTOWN. The well-decomposed woody peat
rests on sand.

MULLICA RIVER CEDAR SWAMP. This bog is located near Pleasant
Mills. The slightly woody peat is underlain by grey, coarse sand.

PORT REPUBLIC CEDAR SWAMP. A well decomposed slightly
woody peat, which includes charcoal to the two-foot level, has a sub-
soil of sand.

HUNTERS MILLS CRANBERRY BOG. The well decomposed slightly
woody peat rests on sand.

UPPER LONGWOOD VALLEY BOG. Located in the valley of the New
Jersey Highlands, this bog developed in the lower limits of the gla-
ciated section of New Jersey. The description of the peat is as fol-
lows according to foot-levels: 0 to 11, reed-sedge-wood; 11 to 14,
aquatic plants; 14 to 15, aquatic plants and wood; 15 to 18, aquatic
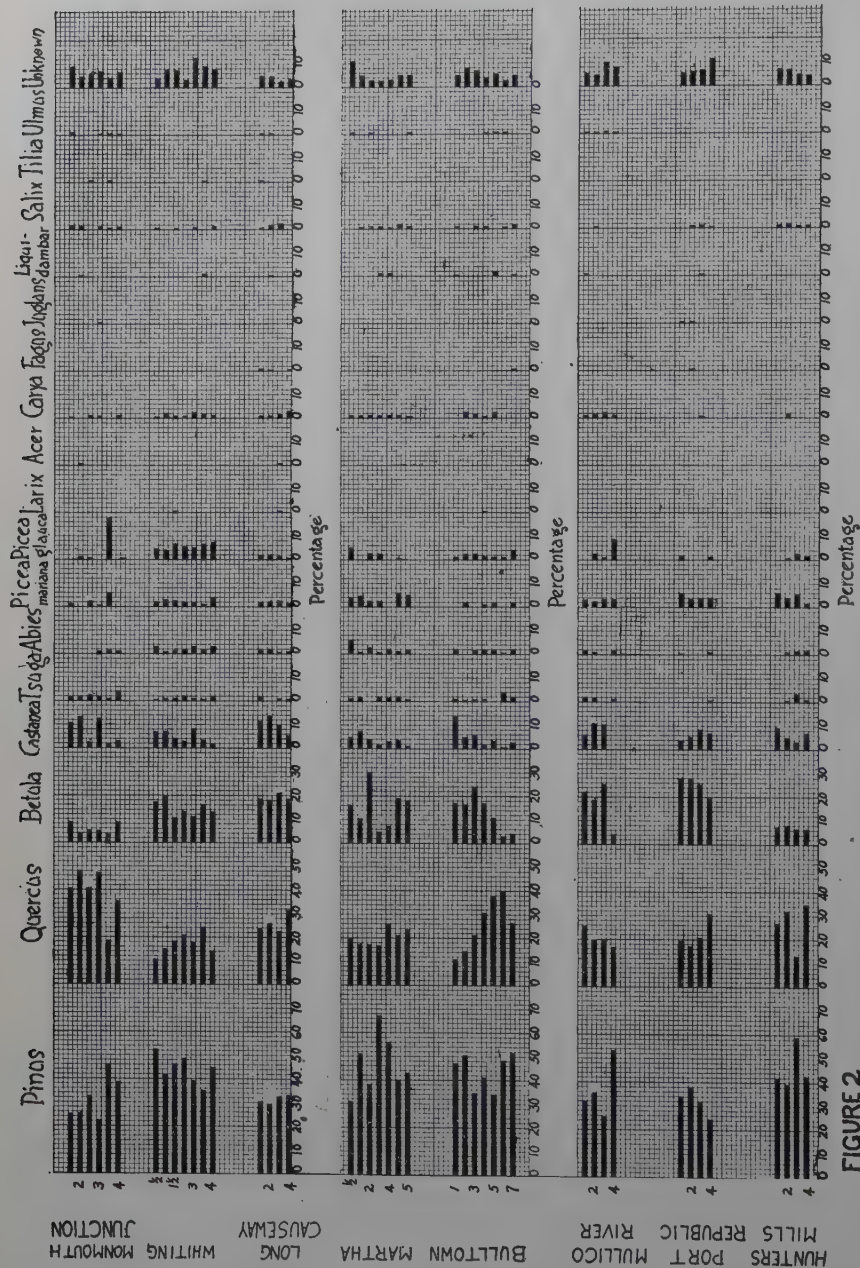sedimentary. The subsoil is clay.

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FIGURE 2

Figure 2. Pollen spectra of tree genera from eight bogs in the Pine Barrens of New Jersey.

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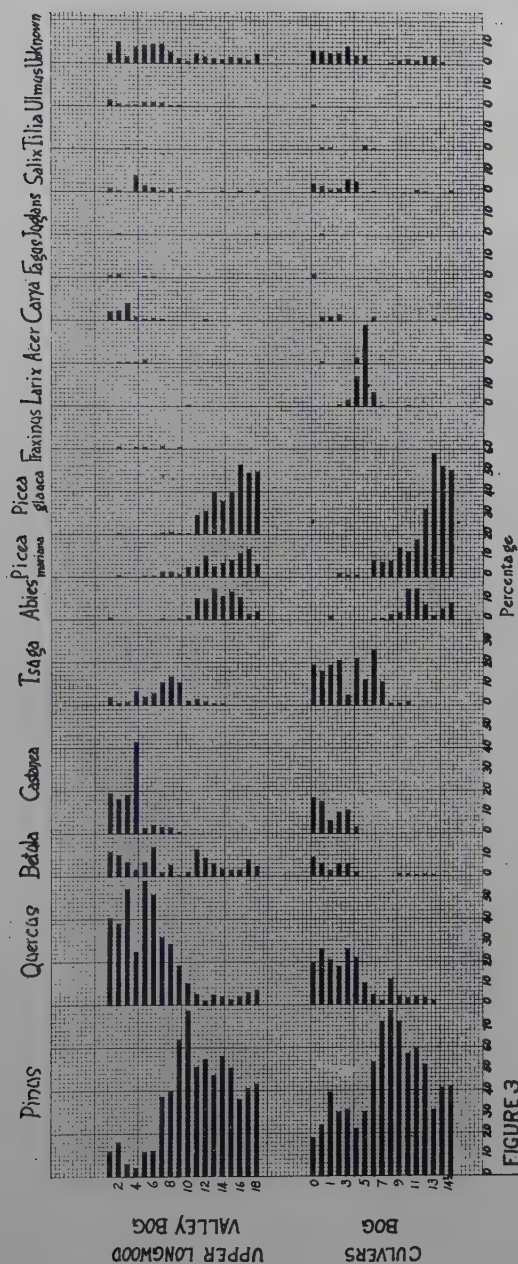
Figure 3. Pollen spectra of tree genera from two bogs in glaciated northern New Jersey.

The first eight of the above bogs involve the greater part of the unglaciated lower section of New Jersey (fig. 1), and so gave hope that some valuable information might be obtained from them relative the characteristics of the forest which existed south of the Wisconsin ice lobe. For an excellent description of New Jersey bogs as a whole the reader is referred to the two books of which Dr. S. A. Waksman is author (19) or co-author (20).

METHODS

The peat was collected in 1942 by men under the direction of Dr. Selman A. Waksman. As a rule, sampling was at one-foot intervals, but at times samples were taken at six-inch intervals (figs. 2, 3). The peat was placed into vials, stoppered securely, and sent to the laboratory at Butler University. Here a permanent label was affixed to the vials, and these were sealed with paraffin. Thus the peat is kept moist, and so lends itself to easy separation for making of slides. Mounts were made according to the Geisler (6) method. A 5% aqueous solution of gentian violet served as stain. Two hundred pollen grains of trees were counted for each foot-level, but pollen grains of shrubs, herbs, and spores of pteridophytes and Sphagnum were tabulated as shown in tables I-III. Pollen grains of Nyssa were not recognized as of this genus until the second count of 100 pollen grains was being tabulated. They are, therefore, shown in the tables as total number for a count of 100 pollen grains. They are not shown on the graphs except as they entered into the number of unknowns in the count of the first 100 pollen grains of trees. The two pollen profiles from Upper Longwood Valley Bog, about 45 miles north of the Monmouth Junction Bog, and about 10 miles south of the Wisconsin end moraine, and that of Culvers Lake Bog, located in the northwestern section of the glaciated area, have been included in figure 2 to show the striking difference in the vegetational history of areas which were influenced by glacial activity and those of the ice-free Pine Barrens.

RESULTS

All eight bogs from the Pine Barrens regions are shallow, none exceeding a depth of seven feet. There is, however, no indication that part of the vegetational history is omitted because of truncated lower portions of the profiles. In a general way, all spectra reflect the same type of forest cover. This is a mixed forest, where coniferous and deciduous species, representing boreal as well as southern

tree genera, were associated. The leading contenders for the crown cover were Pinus, Quercus, Betula, and Castanea. *Picea mariana, P. glauca,* Tsuga, and Abies are no longer extant in the Pine Barrens, and since they have representation even in the topmost foot-levels of the peat, it is very likely that present vegetation cover is not represented in the pollen profiles. A striking feature is that Castanea, Carya, and Tsuga were present when deposition began in the Pine Barrens bogs, while in northern New Jersey (fig. 3) considerable succession had taken place in the forest composition before they entered. (See Potzger and Otto, 1943.) Castanea increased in abundance towards the topmost foot-levels, indicating a moderating climate. *Picea glauca* shows a greater abundance in bogs of more northern location, and to a minor degree Abies and Tsuga express the same feature. Betula was apparently more abundant formerly in the Pine Barrens than it is today. Pinus exceeds Quercus in topmost levels, except in the northernmost Monmouth Junction Bog (fig. 2), indicating approximation of habitat conditions like those of today. Juglans, Liquidambar, Nyssa, Carya, Tilia, Ulmus, Fagus, Acer, and Tsuga were apparently sparsely represented in the forest cover.

Succession can hardly be read into the pollen spectra, for vegetation indicates little change. This may justify the assumption of a more or less static climatic condition. All evidences, however, very strongly suggest that the Pine Barrens constituted a refugium during Pleistocene times, from which the post-Pleistocene wave-like segregation (fig. 3) of associations originated, and ended in a pronounced mixed forest in which Quercus, Pinus, Tsuga, and Castanea played the leading role.

The abundance of grass pollens runs quite high at some foot-levels (tables I, II), but the fact that Alnus and Ilex, as well as ferns and Sphagnum have also left abundant record, the combination indicates lowland habitat sites and extensive wet border areas.

DISCUSSION

When work was first begun on the bogs included in this study the writer had the preconceived idea that the history of the vegetation would approximate that of the border regions of Late Wisconsin glaciation in Indiana, i. e. beginning with a decided Picea period, and evolving through a series of successions. The mixed forest constitution from the lowermost foot-levels was, therefore, at first interpreted as a truncated profile. When all eight bogs yielded the same

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results, and when preliminary investigation of the twenty-foot level of a coastal plain bog located at Tuckerton Bay also lacked the Picea period, while the Upper Longwood Valley Bog (fig. 3), within the lower border of Wisconsin glaciation in New Jersey, showed a decided Picea-Pinus period as initial record, it was concluded that the Pine Barrens or at least the parts which were not covered by water, constituted a refugium during Pleistocene times in which southern deciduous and boreal genera co-mingled, representing a forest border of a type which Transeau (18), Adams (1), and to a lesser degree, also Gleason (8) postulated for central and southern Indiana, but which the writer never found indicated in pollen records from Indiana bogs.

In the post-Pleistocene forest of northern New Jersey pollen records do not report a single genus which did not constitute a major or minor part of the Pleistocene forests in the Pine Barrens region (fig. 2), and three important genera in the post-Pleistocene forests, i. e, Pinus, Quercus, Castanea (perhaps also Betula) represent the leading genera in the Pleistocene forests crouching south of the ice lobe. Others, again, developed from insignificant abundance (Abies, Picea, Tsuga) to major representation in forests which constituted waves of succession as the homogeneous Pleistocene climate south of the ice lobe was superseded by waves of major climatic changes in post-Pleistocene times, and have since vanished from the area which gave them refuge.

Since the succession of forests in Connecticut, as reported by Deevey (3, 4) and in northern New Jersey are so similar (see Potzger and Otto, 1943) one is no doubt justified to assume that from the Pine Barrens region the vegetation migrated north and northeastward. If the ice masses wasted more rapidly along the coastal belt than in the interior central states area, where the ice lobe had swung farther southward, the forests of New Jersey and New England are more ancient than those of the Lakes States, even though their successional history is similar. This would also make unnecessary the migration of broadleaved genera from southern Appalachian centers as postulated by Harshberger (9).

The proper interpretation of grass pollens is still one of the big problems in pollen analysis. As Geisler (7) has shown, the hope of separating aquatic from prairie grasses is slight, if not almost hopeless, because *Zizania aquatica* has pollen of the same size and general characteristics as the dominants in the prairie group. For that reason

it becomes necessary to take various accompanying factors into consideration, which may give aid in the proper interpretation of the meaning of grass pollen representation. In the present study abundance of Alnus, Ilex, ferns, and Sphagnum certainly favors the assumption that aquatic or semi-aquatic species of grasses were the source of the pollen in the peat.

CONCLUSIONS

1. A pollen study of eight bogs located within the Pine Barrens area of New Jersey is presented.

2. The vegetation begins as a decided mixed forest in which genera of the southern deciduous and the evergreen forests associated; and where changes in the forest cover type was small during time in which the peat accumulated.

3. Quercus, Pinus, Betula, and Castanea play the leading role.

4. Carya and Castanea were present at the beginning of sedimentation.

5. Some of the genera no longer present in the Pine Barrens area are: *Picea mariana, P. glauca,* Tsuga, and Abies.

6. Betula is perhaps less prominent now than it was earlier in post-Pleistocene times.

7. All pollen profiles from the eight bogs are strikingly similar, except that Pinus was less important in the topmost level at the Monmouth Junction Bog than in all others.

8. Juglans, Liquidambar, Nyssa, Carya, Tilia, Ulmus, Fagus, Acer, and Tsuga indicate a very scattered representation in the forest complex.

9. The abundant grass pollens at many foot-levels were perhaps contributed by aquatic or semi-aquatic species, for wet habitat is suggested by abundance of such plants as Alnus, Ilex, ferns' and Sphagnum.

10. The dominant phase of the Pleistocene forest in southern New Jersey was perhaps much like that of the present forest, but it had a more heterogeneous composition.

11. Fluctuations are small; this suggests little change in climate while records were accumulating. Increase in Castanea from lower to topmost levels may indicate moderating climate.

12. The thought is advanced that southern New Jersey constituted a refugium during Pleistocene times from which post-Pleistocene migration of forests northward originated.

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TABLE I

(A). Percentage representation of tree genera in a count of 200 pollen grains at a given foot-level.
(B). Actual number of shrub and herb pollens and spores of lower plants, tabulated while counting 200 pollen grains of trees.

(A)	Monmouth Junction								Whiting (Foot-Levels)					Long Causeway					Martha					
	1½	2	2½	3	3½	4	½	1	1½	2½	3	3½	4	1	2	3	4	½	1	2	3	4	4½	5
Pinus	25	25	29½	22	46	38½	57½	42	46	48½	39	35	44½	30½	28	32½	33	31	51	38	67	55½	40	43
Quercus	40½	48	40½	47	18½	35½	10½	15	18	20½	17½	24	14	30½	29	33	33	20	17	17	16½	25½	21	23
Betula	8½	4	5	5	3½	8½	17	20	10½	13	11	16	13	19	17	21	18½	16	30		4½	7½	19	18
Castanea	10½	13	12½	12½	2	3	7	7	4	2½	8	3½	1½	11½	13½	9½	1	5	7½	4	1½	3	3½	1
Tsuga	1½	2	2½	1½	½	4	½	1	1	2½	2	½	2	2	1½	1	½	1	1½	4	2	2	1½	½
Abies				1	1		3	½										6		2½	½	2		1½
Picea mariana	1½		2½	½	2	6	2	3		2½	½	1½	4	2	1½	2½	2½	4	5½	2½	½		5½	1½
P. glauca		1	½	½	17½	17½	½	2½	2	5½	5½	½	7½	1½	1½	1½	1½	5	½	2½	½		½	5
Larix											½						.½							
Acer	½																.½							
Carya	½		1	1	1	1	½	2	1	2½	1½	1½	1½	1	1	1½	1½	1	1	1	1	1	1	½
Fagus			½											½	½	.½								
Juglans				½												.½								
Liquidambar	½																		1			1		
Salix	2	1		1½	1½	1	½	2	½		1	1½		1		2½			½	1½	1	½	2½	1
Tilia		½		½	½						½	½		½	½	.½					½			
Ulmus	1		½	½	½								½	½	½	.½	1	1	5					1
Unknown	9	5	6	7	4	6½	4	7½	7½	3½	12½	9	8	5	4½	2	3½	11	5	3	2½	3	5	.5

(B)	Monmouth Junction								Whiting (Foot-Levels)					Long Causeway					Martha					
	1½	2	2½	3	3½	4	½	1	1½	2½	3	3½	4	1	2	3	4	½	1	2	3	4	4½	5
Nyssa	19	28	1	1	1	1	1		8	2	1	1	1	2	1	3	3	4	8	1	4	4	1	1
Alnus	1	10	27	13	23	28	3	5	2	3	5	5	3	15	7	8	12		8	12	2	1	12	7
Corylus	5	5	2	1	4	3	4	3	3	3	2	2	4	6	7	3	5	3	3	6			15	5
Ilex	38	66	15	11	21	26	22	59	31	35	39	49	52	27	17	17	46	20	21	28	14	9	16	57
Grasses	11	4	7	14	2	36	2	2	52	8	25	37	16	22	46	46	28	3	4	11	2	15	17	29
Ericads			4	3	10		2	2	6		2	4	4	8	3	3	3	20		4	1	4	3	2
Compositae				1					3	1	3	10	10	8										
Chenopods											1		1	24		1	1			1	1			
Fern spores ?	12	14		6		7	3		2	2		1				1				1	1	1		1
Thelypteris	12	14	13						1		1				1	1	2		½	1				
Osmunda	7	3			7				1											1				
Fern spores ?		5	1	2	2	2	2		1	2		2				1			2	1			2	
Sphagnum	32	21	25	11	9	7	34	58	80	30	60	28	66	25	29	19	25	6	29	19	16	22	99	36
Typha																4	2							

TABLE II

(A) Percentage representation of tree genera in a count of 200 pollen grains at a given foot-level.
(B) Actual number of shrub and herb pollens and spores of lower plants, tabulated while counting 200 pollen grains of trees.

(A)	Bulltown							Mullico River (Foot-Levels)					Port Republic				Hunters Mills			
	1	2	3	4	5	6	7	7	1	2	3	4	1	2	3	4	1	2	3	4
Pinus	47	50½	34½	40½	33½	48	51	26½	32	35½	25½	53½	34	38	32	24	42	39½	59	42½
Quercus	11	15	21	30	37½	40	26½	25½	20½	20	16½		19½	17	20½	30	27	32	13	34½
Betula	17	17½	24	16½	10½	3	4	22	18½	25	10½	4	28½	27½	25½	19	7	8	6½	6½
Castanea	14	4½	5½	1½	3	3½	1½	6	10½	10½	10½	4	4	5½	8½	7	9	5	3	7
Tsuga	1	½	1	1		3½	2	1½	1½	1½	1½	1½		½		½	½	½		1
Abies	2	½	1½	1½	1½	½	2	2	1	1	1½	1½				1				
Picea mariana	½	½	1	1	1	1½	1½	2½	3	4	3½	3½	2	2½	3½	6	4	4	1½	6
P. glauca	1	2½	2½	1½	2	1	4	4	2½	1	1	9	6	3½	4	4	½	½	5½	1½
Larix				½	½															
Acer		2½	1½	½					2	3	1							1½		
Carya	½	2½		1½	2½	½		½	2	3				½	½					
Fagus							½						½	½						
Juglans				½									½		½	½				
Liquidambar	½						½	½		½				1	1½					1
Salix	1			1	2		2		1		½									
Tilia																½				
Ulmus				½		½			½	1		½								
Unknown	5	8	7	3½	5½	2½	4½	4½	5	10	8	8	5½	6	6½	11	7	6½	4½	4
(B)																				
Nyssa		1	1	1½	1	2	1	2	1	1	½	2	1	2	1	1	13	20	4	6
Alnus	2	8	8	7	4	2	10	10	5	8	8	8	3½	15	5	20	4	10	60	93
Corylus	1	6	10	3	4	2	3	3	13	6	6	6	½	11	13	13	1	2	3	4
Ilex	2	26	99	35	16	2	18	11	29	23	26	4	18	26	31	21	13	16	3	3
Grasses	41	16	28	12	29	14	36	32	33	26	26	26	23	24	9	10	23	14	14	41
Ericads	1	3	2	1	1		3	10	6	4	4	7	19	4	2	4	80	12	2	
Compositae		1	4	1	1		2		2	3				4	4	2	9	1	1	1
Chenopods				½									2				2			
Fern spores ?																	12	25	22	41
Thelypteris																			8	5
Osmunda		3	1	1		2	1	1	1			1		2		2	2		15	11
Fern spores ?							2	11	21	25		3	3		1	3	3			
Sphagnum	24		12	51	8	6	16	16	1	2	2		3	9	14	12	24	15	10	14
Typha						1														

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TABLE III

(A) Percentage representation of tree genera in a count of 200 pollen grains at a given foot-level.
(B) Actual number of shrub and herb pollens and spores of lower plants, tabulated while counting 200 pollen grains of trees.

Upper Longwood Valley Bog

(A)	Foot-Levels																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Pinus	11½	14	5½	4	11½	12	37	40	63½	77	51	54½	47	56	50½	36	41	43
Quercus	40½	38	54	25	58	51½	31½	28½	18½	10	5	2	4½	4	2½	4	5½	7
Betula	11½	10	6½	3	6½	13½	2	5½	½	2	12½	8½	6	3½	3	3	7½	4½
Castanea	19	16	18	43	2½	4	3	2½	½									
Tsuga	3½	1	1½	6½	4	5½	10½	13½	10½	2	3	1½	½	½	13	10½	2½	
Abies	1						½		½	2	10	9½	14½	11				4
Picea mariana		½		½	½	½	2½	2½	1½	4½	5	10	5	6½	8	11	13½	6
P. glauca		½		1½	½		½	1	½	½	9	11	20	15½	20	32½	28½	29
Larix										½								
Acer		½	½	½	1½													
Carya	4	4½	8	1½	½	1	½						⅓					
Fagus	1	1½			½	½												
Fraxinus		1		1	1		1½		1									
Juglans		½																½
Salix	1½	½		7½	3	2	½	1½		½				½		½		1
Tilia			½		3½				½									
Ulmus	3	1	½	½	1½	2	1½	½	½									
Unknown	4½	10	3	7½	8½	9	9	5	2½	1	4½	3	2½	2	3	2½	1½	4½
(B)																		
Nyssa	1																	
Alnus	7	11	18	22	5	18	2	5	3		16	25		3		1	1	1
Corylus			4	1		5		1										
Ilex	2	3	3	7			1						1					
Grasses	18	18	26	10	13	9	15	3	13	5	4	1	6	1	1	1	10	6
Ericads	9	3	1		8	16	4	4	3		1	1	2	2	1		2	
Compositae		2		1	3	4	5	5	3	3	1		2	6	1	1	2	3
Polypodium								5										
Fern spores ?	1	9			5	3	2	1	1									
Thelypteris	15	13	13	83	44	26	63	3	101	11								
Osmunda		10	15	1	3	1	3	1										
Fern spores ?			5	5	2	2	2	4										
Sphagnum	12	6	23	9	1	1	2							2				
Typha	8	1	2		1	1												